Breeding, survival, movements and foraging of tawny owls strix aluco in a managed spruce forest: a spatial approach

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Breeding, Survival, Movements and Foraging of Tawny Owls *Strix aluco* in a Managed Spruce Forest: A Spatial Approach.

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Abstract

In 1996-98, I studied the spatial ecology of the tawny owl *Strix aluco* (L.) in Kielder, a managed spruce forest in Northumberland, northern England. I employed radio tracking in an individual-based approach, estimating densities of field voles *Microtus agrestis,* the owl's main prey in Kielder Forest, using a calibrated sign index. In both 1996, a low vole year, and 1997, an increasing vole year, juvenile mortality was high, and largely due to starvation and predation. 55.4% of the variation in the mean number of days survived post-fledging per brood was explained by a model comprising the variables mean clutch hatch date, brood size, and voles per hectare at the clear-cuts nearest natal nest boxes in the spring of breeding. Nine percent of non radio tagged juveniles were recruited in 1997-98, in comparison with none of the radio marked individuals. Post onset of dispersal, vole abundance explained 25.7% of the variation in the time that juveniles spent in different areas. Juveniles did not become more sedentary over time nor avoided roosting in occupied territories. Adult home ranges contained more grassy areas than expected from their abundance in the study area, but not from their abundance at watershed level. The absolute areas of grassy habitat and lengths of habitat edge that were included in home ranges varied widely. Range area was correlated with distance to the nearest clear-cut, but not with variation in estimated vole abundance. Nocturnal activity centred on clear-cuts, other grassy areas, and mature forestry plantations. Field voles constituted 59% of prey deliveries to two nest boxes. The time that owls spent at clear-cuts was not correlated with estimated vole abundance there. Tawny owls are generalist predators, but their spatial ecology was strongly influenced by the abundance of their main prey species and the distribution of habitats that supported it.

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I hereby declare that no part of the material offered has previously been submitted by me for a degree in this or any other University. Material from joint work, or from the work of others, has been acknowledged, and quotations and paraphrases suitably indicated.

To my mum, June Coles

Chapter 1 General introduction

1.1 Introduction

How do individual responses to environmental characteristics affect the processes that control the dynamics of natural populations in time and space? This is an important ecological question, and a field of research with considerable practical application. Information gathered by such studies has influenced conservation and management practices applying to not only individual species, but also to whole ecosystems (e.g. Wilcove 1994). Radio telemetry provides unique spatial data on how animals use their environment (Kenward 1987). For example, data on habitat use and foraging patterns of nocturnal species, such as owls, can rarely be obtained in any other way. It also allows survival rates and timing of mortality to be estimated. Modern techniques in information technology, such as Geographical Information Systems (GIS), and software specifically produced to analyse radio telemetry data have further increased the scope of studies using data collected in this way. Together, these technologies allow an individual-based spatial approach to field investigations.

The tawny owl *Strix aluco* (Linnaeus) is a resident generalist predator, and in Kielder Forest, Northumberland, its main prey is the field vole *Microtus agrestis* (Petty 1999). Both species have been studied there since 1980, with most tawny owl breeding attempts confined to the nest boxes provided (e.g. Petty 1992). In 1996, there were 54 occupied tawny owl territories within the study area. Discrete populations of field voles exist in clear-cut patches, isolated within a matrix of older spruce forest. They exhibit three to four year cycles in abundance, which are locally synchronised over distances of around 13-15 km (Sherratt *et al.* 2000).

This unique situation provided a rare opportunity for empirical autecological research. Making extensive use of radio telemetry and taking a spatial approach, this study aimed to investigate the interaction between tawny owls, their prey, and their environment. This chapter begins by giving a basic background to tawny owl biology in the context of this study. Accounts that are more specific appear in the relevant chapters. Then, I briefly introduce the phenomenon of cyclicity in small rodent populations, with specific reference to field voles in Kielder Forest. A statement of specific aims follows a brief introduction to GIS. The results, their interpretation, and

general conclusions appear after an account of general methodology and a description of the Kielder Forest study area.

1.2 Basic biology of the tawny owl

1.2.1 General characteristics

The medium-sized, nocturnal tawny owl (European race, *S. a. sylvatica*) belongs to the Striginae (forest owls), one of the two sub-families in the family Strigidae, which is in turn one of the two families of the order Strigiformes (Cramp 1985). It is the commonest owl in Europe, absent only from Ireland, northern Scotland and some Scottish Islands, northern Russia, northern Scandinavia, Iceland and some Mediterranean islands (Mikkola 1983). The UK population was recently estimated at 20,000 breeding pairs (Stone *et al.* 1997) although, historically, opinion has varied widely from 10,000 to 100,000 (Parslow 1973) and 50,000 to 100,000 (Sharrock 1976) pairs.

Normal weights for British birds are 320-470g and 390-575g for males and females respectively (Hirons *et al.* 1979). Female tawny owls are 26.2% heavier than males and have 4.3% longer wings (Hardy *et al.* 1981). The bird exists in a spectrum of colour morphs, the two extremes being represented by grey and rufous-brown individuals (Petty 1992).

Although tawny owls may hunt in flight (Nilsson 1978) or on the ground (e.g. Redpath 1995), the bird has evolved for life in woodland. Short wings give high manoeuvrability between trees but their relatively high wing loading makes sustained flight costly and, therefore, hunting from perches is more efficient (Petty 1992).

1.2.2 Population and breeding ecology

A large amount of current knowledge of British tawny owl populations has come from the research of various authors working in two long-term study areas. The first, in Wytham Woods, a lowland broadleaved woodland (e.g. Southern, 1970, Hirons 1979, Appleby 1995), and the second in Kielder, a managed upland coniferous forest (e.g. Petty 1992, Appleby *et al.* 1997).

Tawny owl density is greatest in continuous broadleaved woodland, where wood mice and bank voles are relatively abundant (Southern and Lowe 1968). In these habitats, rodent abundance from autumn through to early spring determines whether owls breed and, if they do, how successful they are (Southern 1970, Hirons 1985a). Up to 100% of pairs may refrain from reproducing in years of low vole numbers (Hirons 1976). During the period when growth of ground vegetation made hunting rodents less rewarding, other prey such as invertebrates, birds, moles, and juvenile rabbits were frequently taken. Food supply ultimately determined breeding density, with territorial behaviour being the proximate mechanism (Hirons 1976, Southern 1970).

In Kielder Forest, reproductive output was correlated with the abundance of field voles. These formed 66% (by number) of the prey found in nest boxes from 1979-90 (Petty 1992). Switching to alternative prey when voles are scarce has allowed owls to remain resident in territories, and to maintain relatively stable numbers in comparison with nomadic species (Petty 1992, 1999). However, tawny owl numbers in Kielder Forest have recently declined after peaking in 1991 - the same period that goshawk numbers reached their maximum after first attempting to breed in the study area in 1972 (Petty in prep.). This is one of a number of factors under consideration as a reason for the decrease. Prior to 1991, tawny owl numbers had increased as more foraging habitat was created by clear-cutting (Petty 1989, Petty 1992, Petty *et al.* 1994). In Kielder Forest, territories are regularly distributed along valleys with breeding density declining with altitude. Their boundaries are asserted vocally (e.g. Appleby and Redpath 1997) in September-October, when juveniles of the year are dispersing and trying to locate vacant territories, and then again in January-February, just prior to breeding.

The tawny owl can breed at one year of age, but may be unable to secure a territory until three or four years of age. In Kielder Forest, the mean age at first breeding for female tawny owls was 2.45 years (n =51), the majority breeding for the first time at three years of age. For males (n =25), the respective figures were 2.12 and 2 years (Petty 1992). Territorial males suffered higher mortality than females, allowing earlier male recruitment. In general, more first-time breeding by three-year-olds occurred in years of increasing vole abundance than in declining years of the

vole cycle, in which most first time breeders were yearlings. When vole numbers were at their lowest, the few owls that recruited were two years of age.

A single clutch of eggs is laid at around the end of March, which, if lost due to predation, human disturbance (Petty 1992) or poor weather, may be re-laid (Hardy 1977). The onset of breeding is determined physiologically, with birds in poor condition unable to achieve the gonad maturation necessary for reproduction (Hirons *et al.* 1984). In Kielder Forest, the timing of the onset of egg laying, incubation, hatching and, therefore, fledging were determined by field vole densities in the preceding winter (Petty 1992). Modal clutch size varied from 1 to 5 (2-4 most frequent) depending upon the state of the vole cycle. Thus, variations in both breeding success and recruitment patterns were related to changes in field vole abundance.

The male owl provisions the female and her brood until the latter part of the nestling period when she resumes hunting. The chicks leave the nest at the age of 28-32 days and remain within their parent's territory during a 10-week post-fledging dependence period (Southern 1970, Cramp 1985). Juvenile dispersal begins in mid-July.

Petty (1992) demonstrated the presence of a pool of unrecruited owls (floaters), both males and females, within the Kielder Forest population at certain stages in the vole cycle, although little is known about their behaviour, movements and interactions with the territorial population. Cramp (1985) stated that juvenile tawny owls die if unrecruited. Southern (1970) concluded that young birds that fail to find a territory either starved or moved outside the study area. However, tenancy of vacant territories is rapid (Redpath 1995, Hirons 1985b). This infers the presence of surplus individuals without a territory, since tawny owl nest site and pair fidelity are often assumed to be absolute (Mikkola 1983) and movement of established birds between territories is rare (e.g. Petty 1992). Mate and territory fidelity in Kielder Forest were high, with just 2% of territory holders changing territories (Petty 1992). Only one female and four males moved, and all were relocated in adjacent territories. Recent evidence from Kielder Forest has pointed to increased turnover of the territorial population because of mortality to goshawks (S.J. Petty, personal communication,

also see above). Replacement of territory holders tends to be on a one to one basis, taking place whenever an established owl disappears, thus maintaining the stability of the territorial population (Southern 1970, Petty 1992, Redpath 1995). Accounts of tawny owl biology that are more comprehensive appear in Mikkola (1983), Cramp (1985) and Petty (1992).

1.3 Field vole population cycles

In many northern habitats, populations of small microtine rodents (particularly voles, *Microtus* spp., and lemmings, *Lemmus* spp.) undergo cycles of abundance with a typical periodicity of three or four years (Begon *et al.* 1990). Vole densities in Kielder Forest have been estimated using a simple vole sign index (VSI) at a minimum of 13 grassland sites distributed over the Kielder Block in spring, summer and autumn since 1984 (Petty 1992, Lambin *et al.* 1998, Sherratt *et al.* 2000, Lambin *et al.* 2000). Overall, populations cycled with a periodicity of three to four years, but oscillations in different locations were not entirely synchronous (Lambin *et al.* 1998).The highest growth rates occurred in the summer, but overwinter growth rates were mostly positive and declines occurred in only two winters of a 14-year study period (Lambin *et al.* 2000). The observed spatio-temporal dynamics were consistent with a linear periodic travelling wave. This was estimated to travel roughly along an axis of 72° from grid north at a speed of 14-19 kilometres per year, with local synchrony over distances of 13-15 kilometres (Sherratt *et al.* 2000). Such dramatic changes in the availability of field voles in Kielder Forest have heavily influenced the feeding and reproductive strategies, and population dynamics of Kielder's tawny owls (see above).

1.4 Introducing Geographical Information Systems (GIS)

All data chapters in this thesis make use, to a greater or lesser extent, of Kielder Forest GIS digital databases. GIS technology provides a means of integrating and organising data, and understanding their spatial relationships. A useful simplified definition describes GIS as "a computer system capable of holding and using data describing places on the earth's surface" (ESRI 1993). The major applications of the technology in this study were in referencing aspects of tawny owl ecology to field

vole abundance and habitat characteristics. I give a fuller description of this methodology in chapter 2.

1.5 Aims

This study builds on S.J. Petty's long-term research into tawny owls and field voles in Kielder Forest (Petty 1992). Using radio telemetry, I studied the behaviour of individual birds in detail. The principal aims were to:

i) Investigate some of the factors affecting survival and mortality of juvenile tawny owls

ii) Examine the role of food supply in juvenile dispersal.

iii) Examine space use of territorial adults in relation to habitat characteristics and food supply.

iv) Gather direct information on foraging patterns of territorial adult tawny owls.

The knowledge gained in the course of meeting these objectives is important in understanding the responses of individuals and, collectively, of populations to their environment.

Chapter 2 General methods and study area

2.1 Introduction

This chapter discusses general methods used for data collection and analysis, and describes the study area. I give an account of fieldwork methodology and a short discussion of the analytical techniques employed. I then provide a background to Kielder Forest, including habitat types and climate patterns during the period of this study. Fieldwork took place over three periods, from July to November 1996, March to November 1997, and March to July 1998.

2.2. Fieldwork methodology

2.2.1 Capture of owls

A variety of techniques was employed to catch adult owls so that they could be ringed, measured and radio tagged. S.J. Petty caught breeding males using nest-box traps (Petty 1992). A wooden tunnel with a one-way entrance door at the outside end was mounted flush to the nest box entrance hole. Traps were attached overnight and males were caught as they provisioned the female and her brood, which were supplied with dead farm chicks. One non-breeding bird was caught in a small, modified Chardonneret (cage) trap (Newton 1986), baited with live mice. Brooding females were caught (also by S.J. Petty) with a net, which was held over the nest box entrance until the bird flew out. Exceptionally, females that did not fly from boxes when they were tapped gently were caught by hand.

2.2.2 Radio telemetry

2.2.2.1 Radio tags and attachment

All radio tags, purchased from Biotrack Ltd. (Wareham, Dorset, UK), were of type TW4, with AG 357 battery and harness tubes of 4mm in diameter. They transmitted for approximately one year on frequencies of 173.143-173.973 KHz and had a range of around 1 km over level ground. This varied with changes in the relative position of the bird and receiver, and from a high vantage point, one signal was picked up over a distance of 9 km.

A soft nylon harness was used to fix transmitters to the back of owls (Kenward 1987: figure 5.1b), leaving adequate slack to compensate for further growth in the case of nestlings. The combined mass of the radio and harness was 7.3g, which

represented 2.0% and 1.4% of the respective mean body weights of adult males and females caught in Kielder Forest (Petty 1992), well within the recommended 5% limit for birds (Caccamise and Hedin 1985).

2.2.2.2 Telemetry equipment and methodology

TRX 1000S (Wildlife Materials Inc., Illinois, USA) and Telonics TR2 (Telonics, Arizona, USA) receivers were used with a hand-held three-element Yagi antenna (Biotrack Ltd.) to find the position of radio tagged birds. The Telonics receiver was used with headphones.

Triangulation was performed using the loudest signal method to estimate receiver-tag bearings (Springer 1979). These were taken from landmarks or pre-determined sites that were marked on trees, deer fences and other immovable features, using high visibility red and white plastic tape. The locations of such fixed "bearing points" were measured accurately using a 30m measuring tape and were double-checked on a 1:10 000 forest stock map. These high quality maps were used throughout the study for plotting bearings and fixes.

The intersection of two or more bearings plotted with their associated angular error to either side (error arcs) forms an error polygon. A polygon formed by two arcs has a 90% probability of containing the animal (Springer 1979). This is reduced to 86% for the intersection of three arcs, but increases to 99% if the polygon is expanded to include the all the intersections of three arcs (Springer 1979: figure 2c).

Error polygons are smallest where readings intersect at 45° (Heezen and Tester 1967) and 60° angles (Springer 1979) for two and three-bearing fixes, respectively. Thus, bearing points were arranged around habitat features (blocks of trees for example) to maximise the potential for obtaining consecutive bearings at these angles, and minimise the distance between transmitters and receivers, so as to produce the smallest possible error polygons.

Following Redpath (1995), sampling error was quantified by estimating roosting positions of owls by triangulation and then tracking them until seen, or their roosting tree was located. Accuracy of bearings has two components - error and precision (Lee

et al. 1985). Error of a consistent nature is termed bias and was calculated as the mean deviation of test bearings from true bearings, including their respective polarities. Sampling error (precision) is the difference between the estimated bearing and the true bearing and was represented by the standard deviation of bias (a fuller account of these calculations is given by Springer 1979).

For 45 bearings representing 15 three-bearing fixes, mean magnitude of error was 4.93° (SE ±0.22). Bias was 0.18°, with an associated sampling error of ±5.19°. Thus, bearings were plotted with ± 5° error arcs, after subtracting 5° to correct for magnetic variation. All bearings were taken less than 500m from the bird, and the majority were within 200-300m, representing not more than ±30m positional error for any one bearing (based upon 300m tag-receiver distance *d*, sampling error calculated at 5.19°, and the formula: error per bearing in metres = SQRT(((*d*/COS(5.19*PI/180))^2 – d^2). Of course, errors for multiple bearings were additive and formed error polygons that varied in size according to the angles of intersection. Such errors were probably caused by the effects of dense geometrically shaped tree stands, water bodies, and undulating topography upon signals.

This study used a quality scoring system for fixes, based upon the following criteria:

1 = sighting.

2 = bird located to tree

3 = triangulation with three or more bearings to produce an error polygon of 1 ha or less, or tracking location to forest sub-compartment (section 2.3.2) level (birds were sometimes disturbed as their roosting site was approached, and moved without being seen).

4 = triangulation with two bearings, the error polygon measuring 1 ha or less.

Most "tracking" fixes were on juveniles and fell within categories 1-3 (table 2.1). The majority of triangulated fixes fell within category three, because most of this type were of adults at night-time when birds were not approached closely and sightings were rare (table 2.1). Any fixes with error polygons larger than one hectare were rejected.

Table 2.1. *Distribution of fix quality for juvenile and independent adult fixes. Adult fixes were mainly triangulated whereas juvenile fixes were derived mainly from direct tracking.*

	Adults		Juveniles		Total	
Quality	*n*	%	*n*	%	*n*	%
1	17	2.5	405	30.1	422	20.9
2	25	3.7	736	54.6	761	37.8
3	462	69.2	202	15.0	664	33.0
4	164	24.6	4	0.3	168	8.3
Totals	668	100	1347	100	2015	100

2.2.2.3 Automatic location system

An automatic location system, based on the quasi-Doppler principle (Angerbjörn and Becker 1992, Schober *et al.* 1992), was field-tested at the beginning of the study. It was hoped that the system would provide large amounts of movement data on a number of adult owls. However, the undulating topography, thick tree cover and climatic conditions of the Kielder Forest study area (section 2.4.4), in combination with underpowered radio tags, caused unacceptably high levels of error, and its use was discontinued.

2.2.3 Prey abundance

Relative densities of field voles were estimated using vole sign indices (VSIs)(Petty 1992). A 25cm^2 quadrat was thrown randomly 25 times within a 0.25ha patch of grass-dominated clear-cut where mature spruce had been harvested, or another suitable area of *Deschampsia cespitosa* dominated grassland. The position of each quadrat differed and was determined by walking 15-25 paces from the previous assessment before throwing again. Within these metal squares, the presence (score = 1) or absence (score = 0) of fresh (green) grass clippings in vole runs was noted and each patch assigned a score out of a maximum 25. Bank voles *Cleithrionomys glareolus*, which occurred widely in the study area but were rare on grass-dominated clear-cuts, do not produce grass clippings and therefore VSIs reflect only field vole activity.

The VSI method has been validated by comparing live-trapping data with index scores at the same sites using linear regressions (see below). These were used to

convert VSI scores into density estimates. The relationship between vole numbers and VSI scores was imperfect, and the degree of variation about estimates is given in table 2.2. Formulae were adjusted to correct for seasonal variation in decay rates of clippings, and show standard errors of parameter estimates in brackets (Lambin *et al.* 2000):

Spring (Mar-May)	n/ha = 13.10(1.76)*VSI+9.96(11.16)	$r^2 = 0.62$	P <0.001
Summer (Jun-Aug)	n/ha = 14.11(1.33)*VSI+14.60(9.34)	$r^2 = 0.71$	P <0.001
Autumn (Sep-Oct)	n/ha = 13.48(1.52)*VSI+23.17(12.67)	$r^2 = 0.72$	P <0.001

2.2.4 Sexing juveniles.

Blood samples were taken from the brachial vein of nestlings by Dr. B.M. Appleby. The sex of each bird was determined using a technique based on female-specific minisatellite fragments (Appleby *et al.* 1997). These data were incorporated into chapters three and four.

2.3 Data analysis

2.3.1 Radio telemetry analysis

All home range and related analyses were performed using Ranges V version 1.00 (Kenward 1995). In addition, some graphics were produced using Tracker version 1.1 (1997, Radio Location Systems AB, Stockholm, Sweden) because its Windows-based approach was more amenable to image manipulation packages.

2.3.2 GIS

Arc/Info version 7.1 (1998, ERSI Inc., California, USA) GIS software on a Unix platform, with ArcView version 3.0 (1996, ESRI Inc.) on PC were used for processing and analysis of spatial data. The GIS held silvicultural (polygon) data at a sub-compartment level, based on Forestry Commission digital databases compiled by C.J. Thomas. These databases were assembled in 1996, so any changes to the study area since then were noted and alterations made accordingly.

Forestry Commission stock maps were divided into compartments. These were units of forest area delimited by planting date, or geographical features such as natural boundaries and roads. These units were further divided into "sub-

Table 2.2 *Conversions of VSI scores to densities. I calculated calibration errors using standard errors of parameters in regressions between VSI and live-trapping estimates of vole density (Lambin* et al. *2000).*

VSI	Seasonally corrected vole density, voles ha^{-1}					
	Spring		Summer		Autumn	
	Voles	SE	Voles	SE	Voles	SE
0	10	11	15	9	23	13
1	23	13	29	11	37	14
2	36	15	43	12	50	16
3	49	16	57	13	64	17
4	62	18	71	15	77	19
5	75	20	85	16	91	20
6	89	22	99	17	104	22
7	102	23	113	19	118	23
8	115	25	127	20	131	25
9	128	27	142	21	144	26
10	141	29	156	23	158	28
11	154	31	170	24	171	29
12	167	32	184	25	185	31
13	180	34	198	27	198	32
14	193	36	212	28	212	34
15	206	38	226	29	225	35
16	220	39	240	31	239	37
17	233	41	254	32	252	39
18	246	43	269	33	266	40
19	259	45	283	35	279	42
20	272	46	297	36	293	43
21	285	48	311	37	306	45
22	298	50	325	39	320	46
23	311	52	339	40	333	48
24	324	53	353	41	347	49
25	337	55	367	43	360	51

compartments" of uniformly planted areas of different species, species mixtures, or crops with slower growth. Thus, compartments and sub-compartments were tools that allowed the forest area to be divided into manageable blocks for planning or management purposes.

Positional data, such as telemetry fixes and vole abundance assessment locations, were built into point coverages, and areal data, such as home ranges, were built into polygon coverages. In both cases, these were created in Arc/Info with the GENERATE program using input from text files. Topology was then built using the BUILD command. Attributes were added to point or polygon coverages using the Arc DBASEINFO command in Arc to import data in dBase format and then the JOINITEM command to add new fields to polygon or point attribute tables. In this way, vole abundance scores, dates and bird identities, for example, were associated with their respective coordinates. During data analysis, the query building facility in ArcView was used to display features according to their attributes. For example, vole abundance scores were displayed by season, and telemetry fixes by date. Further techniques that were specific to a particular part of the study are detailed in the respective chapters.

2.3.3 Statistical analyses

Statistical analyses were performed using Systat 8.0 (1998, Systat Inc., Illinois, USA) and SPSS 9.0 (1998, SPSS Inc., USA) statistical packages for personal computers. Most figures were drawn using either SigmaPlot for Windows version 4.01 (1997, SPSS Inc.), Microsoft Excel (1997, Microsoft Corporation, Seattle, USA) or the statistical packages mentioned above.

The 5% threshold ($P = 0.05$) was used for rejecting a null hypothesis, and the 10% threshold ($P = 0.10$) was sometimes used to indicate a non-significant trend. All statistical tests were two-tailed unless otherwise stated. Normally distributed data were analysed using parametric tests and non-parametric tests were used for data that were not (or not known to be) normally distributed, including data that resisted normalisation by transformation. The notation listed below was used when presenting results, and other abbreviations were defined when used.

n sample size

df	degrees of freedom
SD	sample standard deviation
SE	standard error of the mean
P	probability
CV	coefficient of variation

2.4 Study area

2.4.1 Introduction

Kielder Forest (55' 15 N, 2' 35 W), situated in the centre of Kielder Forest District, is owned and managed by the Forestry Commission. It is situated entirely in the upper valley of the River North Tyne, which lays mid-way between the Solway Firth on Scotland's west coast and the North Sea on the east coast (figure 2.1). One thousand hectares of the valley below 185m above sea level were flooded in 1981-82 to form Kielder Water, Europe's largest artificial reservoir (plate 2.1).

2.4.2 Topography and geology

The altitudinal range extends from 185m at the level of Kielder Water to the summit of Deadwater Fell at 569m, lying to the north of the study area. Unplanted heather *Calluna* moorland to the south-west, north-west and north-east of the study area rises above rolling hills with grazed sheepwalk. Most crags occur along the eroded valleys of several large streams that flow into Kielder Water.

The geology is mainly sedimentary, originating from the Lower Carboniferous series (Robson 1965). Fell sandstones form much of the higher ground around the upper catchment of the River North Tyne. The lower ground towards the north is formed from Cementstones, which lay under the fell sandstones. Both of these groups lie on top of the Scremerstone Coal Group, which comprises the southern half of the study area. The Cementstone and Scremerstone groups include base-rich layers of shales and limestones, while the latter group also has coal seams.

Much of the solid geology was concealed by glacial boulder clay, deposited over a great deal of the study area at the end of the last ice age. Water action has eroded these deposits on the higher moors and upper sill slopes.

Figure 2.1. *a) Location of Kielder in the United Kingdom, and b) location of the Kielder Forest study area in northern England, denoted by a black rectangular box. Kielder Water Reservoir and the outline of Kielder Forest District (green) are shown. The red square represents the location of Kielder Castle weather recording station.*

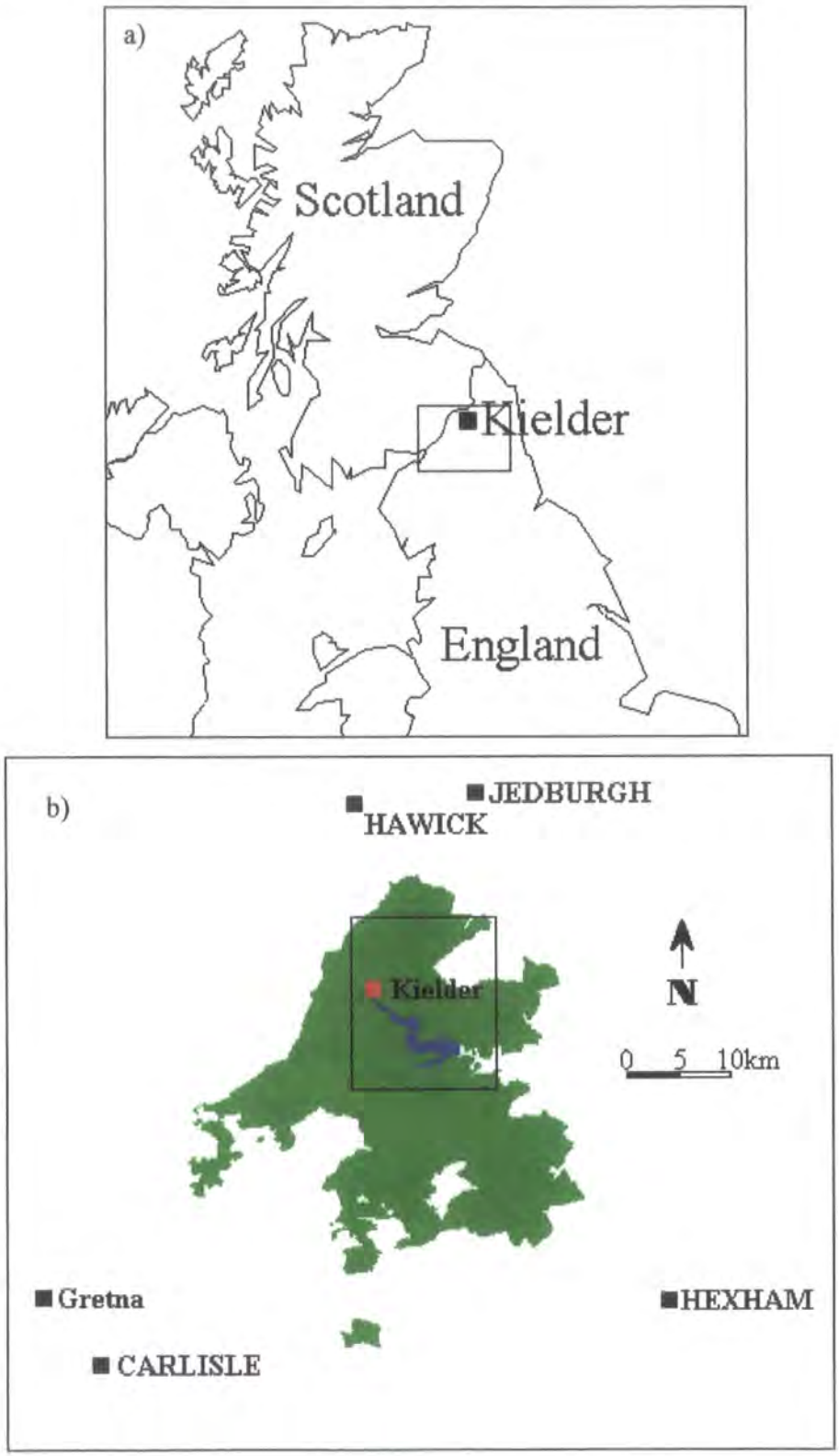


Plate 2.1. *A view west across Kielder Water in the centre of the Kielder Forest study area. The foreground shows a grassy clear-cut, bordered by coniferous tree crops of a variety of species and ages. In the near distance are two typical Sitka spruce monocultures. The higher ground in the far distance marked the western boundary of the study area.*

2.4.3 Land use

2.4.3.1 General characteristics

Better soils occur in lower areas, which were planted first, progressing later to the open moors. Felling and restocking rates of 1000 ha p.a. have occurred in Kielder Forest District since commencing after severe gales in 1968 caused extensive wind throw (Holtam 1971). However, the area to the north of the study area, where territorial adult tawny owls were studied, was not heavily harvested during the 3 years of this study.

2.4.3.2 Broadleaves

The few deciduous trees in Kielder Forest occupy relatively small areas in steep-sided burns and crags. In addition, broadleaves have recently been planted in several areas, and natural regeneration has occurred where conditions (namely deer management) have allowed. Deciduous trees are not grown commercially but are valued for their potential environmental and recreational benefits.

2.4.3.3 Conifers

Conifers comprise almost all of Kielder Forest, which is dominated by non-native species such as Sitka spruce *Picea sitchensis* (75% of the forest area), Norway spruce *Picea abies* (14% of the forest area) and lodgepole pine *Pinus contorta* (7% of the forest area). These are planted in large, continuous block monocultures, which are intensively managed through close spacing and thinning to provide a high yield of straight trees of a constant size, required by industry. Other tree species formed insignificant proportions of the whole.

Planting occurred over a relatively short time interval, so that significant variation in conifer age-classes is lacking in Kielder Forest. This lack of diversity has recently been identified as undesirable, and a large restructuring process is underway. The practices of felling and restocking have presented managers with an opportunity to redesign the forest. Even-aged plantations will be transformed into a mosaic of different aged crops, interspersed with open space and corridors of deciduous woodland along watercourses, resulting in an expansion of the range of successional stages present in the forest at any one time.

2.4.3.4 Forest succession

The relatively fast growth rate of Sitka spruce compared with other trees results in rapid habitat changes over a short time period. Each successional stage has its own associated wildlife community, and different values for tawny owls (Petty 1992). In the **establishment (pre-thicket) stage**, dense ground vegetation develops in association with newly planted crops up to 1m in height (mean height of the 100 largest girthed trees per hectare). The ground vegetation supports small mammal populations, making these areas suitable for foraging tawny owls. Young trees provide potential hunting perches. As trees reach **thicket stage** (3-10m top height), the canopy begins to close and most ground vegetation is lost. Low small mammal populations and the difficulty of flying through these crops reduce their attractiveness for tawny owls. The **pole (pre-felling) stage** (over 10m until felling) sees the re-establishment of some ground vegetation, as wind throw (in exposed areas) and progressive thinning (removal of some trees in sheltered areas, from the late thicket stage onwards) allow light to penetrate to the forest floor. Tawny owls nest and roost in these crops, and they provide a food supply in the form of birds and a limited number of small mammals. Some crops are left to mature beyond the normal felling age (**extended rotation**). The continued growth of ground vegetation increases the suitability of this habitat for bank voles and wood mice *Apodemus sylvaticus*.

2.4.4 Climate

This section provides the climatic setting for the three years of my study. Meteorological data from Kielder Castle recording station (55' 23 N, 2' 58 W, 201m a.s.l.) were taken directly from the UK Meteorological Office.

2.4.4.1 Precipitation

Mean annual precipitation in the years 1996-98 was 1302.7mm. There was no significant difference among monthly precipitation totals in the three years (ANOVA, $F_{2,32} = 0.37$, $P = 0.70$). March to September were the driest months, with least precipitation occurring in June (figure 2.2). There was a sharp increase in October, dropping again in January and rising to a peak in February. An exceptionally high amount of rainfall in February 1997 increased the mean value for that month. If only data from 1996 and 1998 were included, February had an average precipitation of 110.9mm.

Figure 2.2. *Mean monthly precipitation at Kielder Castle recording station, 1996-98. Values are shown ± 1 SE.*

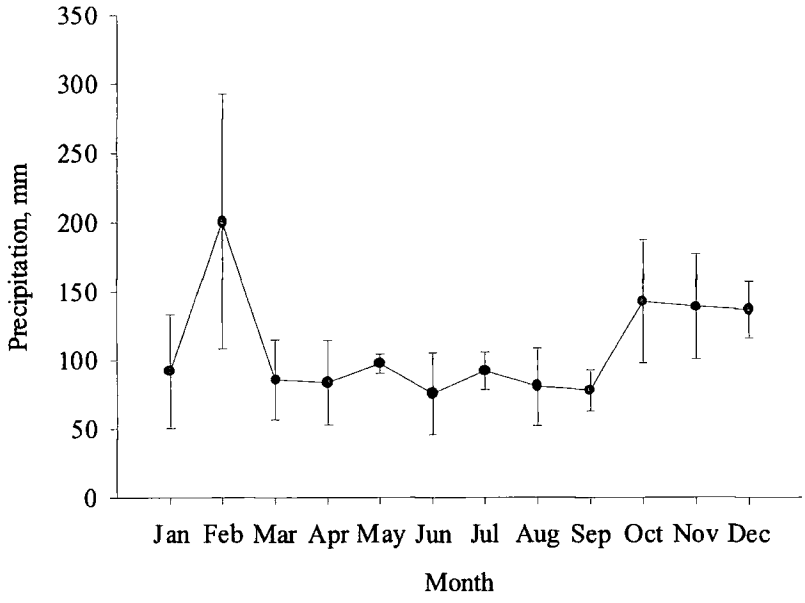
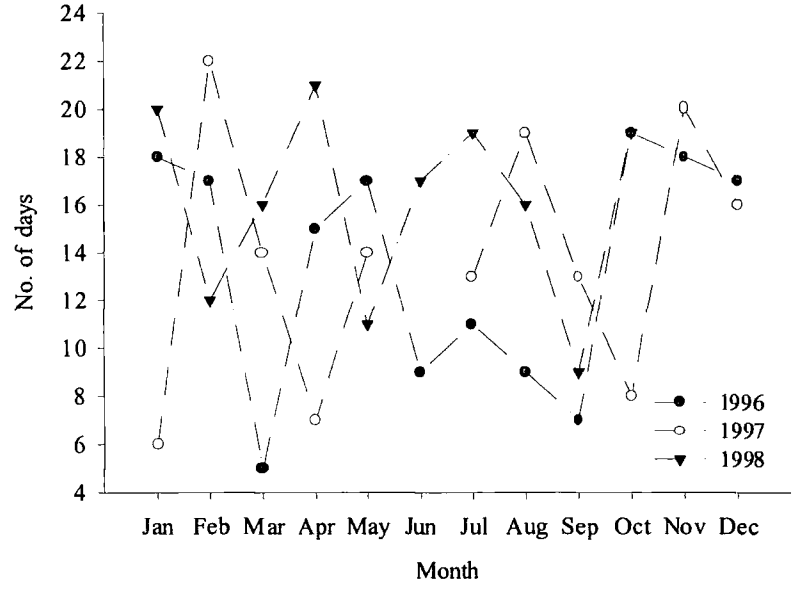


Figure 2.3. *The number of wet days per month at Kielder Castle recording station, 1996-98. A wet day occurred when daily precipitation reached 1.0mm or more.*



The number of wet days per month (when precipitation of 1.0mm or more was registered in the 24 hours preceding 0900H) ranged from five in March 1996 to 22 in February 1996 (figure 2.3). Mean values were 13.5 (SE 1.4) days per month in 1996, 13.8 (SE 1.6) in 1997, and 16.0 (SE 1.3) in 1998.

Snow days were defined as the number of days per month in which at half of a representative area of ground was covered by snow. Thirty-three occurred between November and March 1996, with a maximum of 11 in November. These data were unavailable for 1997. In 1998, nine snow days occurred between December, which had five, and March.

2.4.4.2 Temperature

There was no significant difference among years in maximum or minimum air temperature (ANOVA, maximum: $F_{2,32} = 0.28$, $P = 0.76$; minimum: $F_{2,35} = 0.25$, $P = 0.784$). Mean monthly air temperature peaked at 19.3 °C in August with a low of -0.8 °C in January (figure 2.4). In general, the first frost day, when air temperature at 0900H was at or below 0°C, was recorded in October and the last in March (figure 2.5). When frost was recorded, the number of days ranged from 1-14 per month.

Figure 2.4. *Mean maximum and minimum monthly air temperatures at Kielder Castle recording station, 1996-98. Values are shown ±1 SE.*

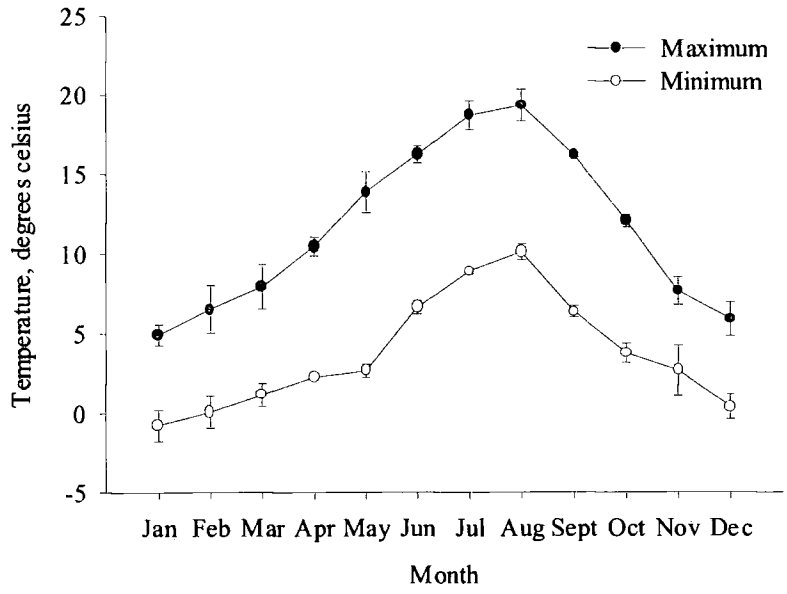
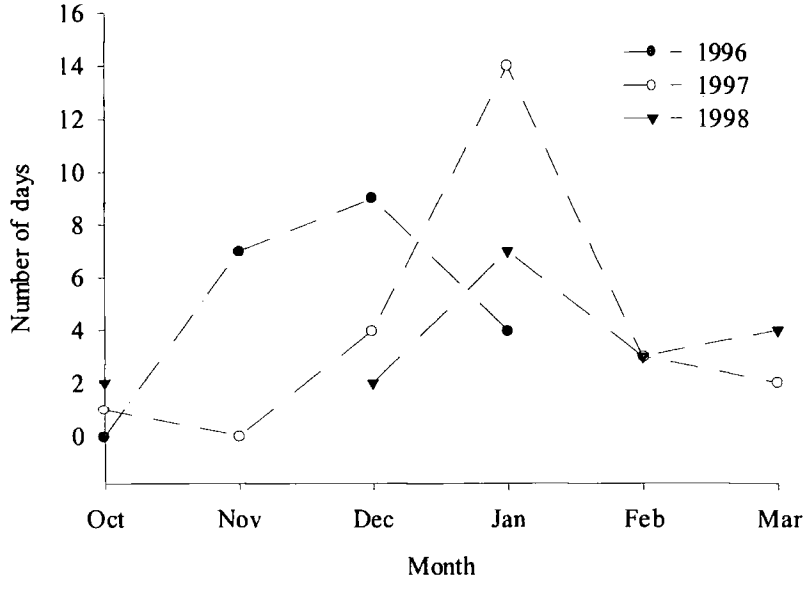


Figure 2.5. *The number of frost days per month at Kielder Castle recording station, 1996-98. Frost days were defined as when the air temperature was at or below 0°C at 0900H.*



Chapter 3 Survival and mortality in juvenile tawny owls: direct and indirect influences

3.1 Introduction

Reproductive success by birds is usually measured by the number of young that fledge (Clutton-Brock 1988, Newton 1989), or the number becoming independent (e.g. Nol and Smith 1987). However, the use of these measures as indices of productivity has been questioned, given the heavy mortality suffered in the post-fledging period (Spear and Nur 1994). The correlation between the number of young produced and those that are recruited is usually poor (Nur 1991), and most bird species have lower survival rates in their first year of life (Lack 1954, Newton 1979). In owls, high losses occur when juveniles become independent and begin to disperse (e.g. Southern 1970, Hirons *et al.* 1979, Rohner and Hunter 1996).

Food shortage is an important factor regulating bird populations, operating chiefly through changes in density-dependent mortality of juveniles (Lack 1954, 1966). Considering the life of a young owl, for example, variation in food abundance begins to affect its future even before egg laying. Petty (1992) showed that female tawny owls in Kielder Forest only bred if food supplies were sufficient for them to reach the critical body condition referred to by Hirons *et al.* (1984). The timing of breeding, and clutch and brood sizes of those which did attempt to breed were closely correlated with relative field vole abundance.

A key assumption in life history theory is that an increase in resource allocation to offspring will increase offspring fitness (Dangerfield 1997). After hatching, the development of the young bird is critically affected by its food supply and juvenile survival is sometimes positively correlated with pre-fledging mass (e.g. Magrath 1991, Gaston 1997). Consistent with this, Overskaug *et al.* (1999) found that in juvenile tawny owls from a Norwegian population, post-fledging survival was correlated with fledging mass. Southern (1970) demonstrated how brood size interacted with food supply and affected mass gain of tawny owl chicks, with broods of two young having an advantage over both larger and smaller broods of the same year.

The affects of variation in prey abundance upon nestlings are mediated via its availability. For example, weather conditions can affect the ability of adults to detect and obtain prey. Appleby (1995) found that the speed of tawny owls' movement was affected by rain, wind, surface moisture and cloud. Heavy rain, strong winds and thick cloud were expected to impair the hearing and vision of owls, thus decreasing hunting performance. Short-eared owls *Asio flammeus*, for example, required significantly less time to search for and capture deermice *Peromyscus maniculatus* as illumination from moonlight increased (Clarke 1983). The deermice were correspondingly less active in bright moonlight. Variation in activity patterns in *Microtus* may be associated with energy costs (Reynolds and Gorman 1994). Drabek (1994) showed that nocturnal activity increased in summer, possibly as a consequence of high daytime temperatures. These factors may affect *Microtus*' availability to predators. The extreme negative effects of even a very short temporary reduction in food supply to tawny owl nestlings during the most rapid period of growth (from hatching to around 16 days of age) was illustrated by Southern (1970).

The ability of perch-hunting predators to catch prey also varies with habitat structure (e.g. Southern and Lowe 1968, Nicholls and Warner 1972, Sonerud *et al.* 1986, Kullberg 1995, Malan and Crowe 1997), and perch characteristics and availability (e.g. Sonerud 1992, Kullberg 1995, Malan and Crowe 1997). For tawny owls, daylength determines onset of hunting activity and restricts the time available for foraging in summer (Hardy 1977). However, diurnal hunting has been recorded (summarised by Mikkola 1983 and Cramp 1985, personal observation).

In many owl species, including the tawny owl, factors associated with parental hunting success continue to affect fledglings for the extended three-month post-fledging dependence period. It is also during this period that food abundance may interact with predation, for example, to influence survival. The relatively slow development during this period may lead to increased susceptibility to disease and other mortality factors, such as predation (Rohner and Hunter 1996) and parasitism (Appleby *et al.* 1999) when under environmental stress. In addition, defence responses of adults adult tawny owls increase in very good food years (Wallin 1997, S.J. Petty, personal communication).

In Kielder Forest, year-to year recruitment patterns were heavily influenced by prevailing field vole densities (Petty 1992), with starvation identified as one of the chief causes of mortality in juvenile tawny owls, (Southern 1970, Hirons *et al.* 1979, Petty and Thirgood 1989, Overskaug *et al.* 1999). The highest recruitment occurred in low and increasing vole years, when juvenile dispersal coincided with high vole abundance over winter. Extremes of 0% and 29% of birds from any one cohort were recruited in Kielder Forest, and in the low and declining phases of the vole cycle, the hatch dates of recruited chicks were earlier than those of their unrecruited counterparts.

Korpimäki and Lagerström (1998) also found that food conditions during the post-fledging and independence periods seemed to be crucial for the survival of young Tengmalm's owls *Aegolius funereus,* with a selective advantage for owls which invested most in reproduction during the increase phase. However, hatching date within the season did not seem to affect survival.

Another factor that has been considered in avian survival studies that have used telemetry is the potentially detrimental mass burden imposed by radio tags. Paton *et al.*(1991) asserted that radio tags adversely affected the survival of female spotted owls *Strix occidentalis*. They cited work by Caccamise and Hedin (1985), which suggested that energetic costs of carrying radio tags were greater for larger birds, as a possible explanation, given the reversed sexual dimorphism of the species.

This chapter examines some of the possible influences of juvenile survival outlined above. I also examine the timing and causes of mortality. Work took place in 1996, a low vole year, and 1997, an increasing vole year. Food supply during dispersal was not compared with survival because birds experienced a variety of prey densities. The role of food supply in the post-fledging and dispersal behaviour of juvenile tawny owls is investigated in chapter 4. Chick condition indices were not included because the timing of pre-fledging measurements was not standardised. Sections on the effects of radio tagging and mortality drew upon data presented in Petty *et al.* (in prep.), and Coles and Petty (1997) respectively.

3.2 Methods

3.2.1 Prey abundance

Vole sign index (VSI) assessments were performed throughout the study area in spring (March), summer (May/June) and autumn (September) (S. J. Petty), spring and autumn (J.L. MacKinnon), and summer and autumn (C.F. Coles). I used the value for the area of suitable grassland nearest the nest box of each territory (figures 3.1 and 3.2) in the spring, summer, autumn and preceding autumn of each breeding attempt, and converted each to a density estimate using a seasonally adjusted formula (Lambin *et al.* 2000, chapter 2). Exceptions to this rule occurred in four territories in some seasons where more than one assessment was available for a clear-cut, for example, when trapping grids were set up. In these instances, mean values were used. A small amount of data were unavailable where assessments had not been performed at the nearest suitable site to a nestbox in some seasons.

3.2.2 Timing of breeding

Hatching date was used as an indication of the relative timing of breeding, where 1 = 1 March. Nest boxes were checked fortnightly from mid March. Eggs and nestlings were weighed and measured, and hatching dates were estimated using a wing length/age growth curve (S.J. Petty, unpublished data).

3.2.3 Radio telemetry

In 1996, when the modal brood size was two, 22 nestlings (of a total of 48 chicks which fledged) from 11 two-chick broods were radio tagged. In 1997, 33 birds were tagged of the 98 that fledged in total. This total was composed of nine broods of three, two broods of two and two broods of one, including 10 of the territories used in 1996. The study broods were distributed throughout the study area (figures 3.1 and 3.2).

Near to fledging, nest boxes were monitored daily so that fledging dates (defined as the day on which a nestling left the nest box, rather than the day of first flight, and where 1 = 1 March) were pinpointed to within one day. Daytime roost positions of juvenile owls were determined every one to three (mean 2) days during the pre-dispersal period, and thus timing of mortality during this phase was usually estimated

Figure 3.1. *Locations of VSI sites (crosses) and nest boxes of radio tagged (red stars) and non-radio tagged (black dots) broods in 1996.*

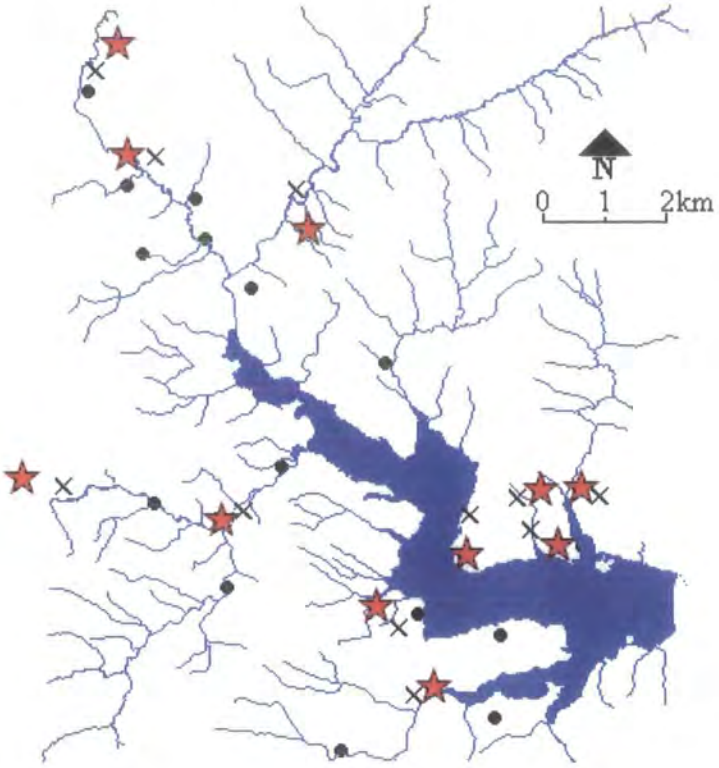
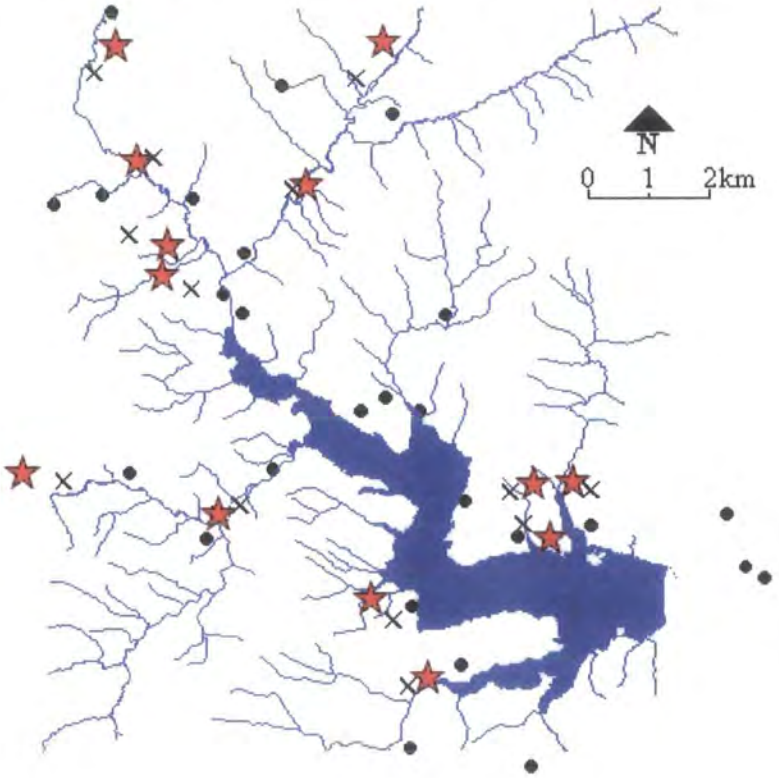


Figure 3.2. *Locations of VSI sites (crosses) and nest boxes of radio tagged (red stars) and non radio tagged (black dots) broods in 1997.*



to within a few days. However, during dispersal, the mean period between fixes increased (table 3.1) because contact was lost with some birds for extended periods, particularly in 1997 when the larger sample size limited search effort per bird. A breakdown by quality of the total number of fixes obtained appears in chapter 2 (section 2.2.2.2). Recovery of corpses or remains of dead birds allowed timing and, in most cases, causes of deaths to be recorded. Two birds were recovered over a month after contact was lost with them, and after they had left the natal territory. In both cases, emaciated remains were found near the last determined location. Time of death was estimated at the time of loss of contact and the cause of death was recorded as unknown.

3.2.4 Factors affecting survival

SPSS GLM was used to construct Type III general linear models to explain variation in days lived after fledging. The distribution of residual values was inspected to assess the appropriateness of models. Seasonal vole abundance, year, hatching date and brood size were considered as explanatory variables (table 3.2). The analysis was applied to 18 broods that were represented in the groups whose remains were recovered. Thus, mean values of variables were used where more than one bird from any one brood was included. Hereafter, relative "survival" of juveniles is discussed in terms of the number of days lived after fledging. Broods of one and two chicks from 1997 were combined into a "less than modal brood size" category.

As a simple test of the null hypothesis that either sex was just as likely to be found dead as the other, I calculated expected frequencies by taking the total number of birds of both sexes found dead in each year and multiplying each value by the proportion of females in each study group. A chi-squared test was then performed on the resulting observed and expected frequencies of females appearing in the groups of birds found dead.

Cox regression analysis builds predictive models that incorporate covariates of survival. Implicit to the Cox procedure is the "proportional hazards assumption", which is that where two sample groups are being compared, the ratio of hazards (deaths) for any two cases will be constant for all time points. In other words,

Table 3.1. *Sampling frequencies after the onset of dispersal for juvenile tawny owls radio tagged in 1996 and 1997.*

Year	*n* birds	*n* fixes	Days between fixes				SE
			Min	Max	Median	Mean	
1996	9	118	1	32	7.8	5.0	2.7
1997	17	236	1	40	1.3	11.0	3.5

Table 3.2. *Variables considered in GLM models to predict days lived after fledging for broods of radio tagged juvenile tawny owls that were known to have died. Mean values of variables were used where more than one bird from any one brood was included.*

Category	Variable	Description
Independent (response) variable	LIFE	Mean brood survival, days lived post-fledging
Categorical covariates	YEAR	Year of study – 1996 (1) or 1997 (2)
	BROOD	Modal brood size (0), < modal brood size (1).
Timing of breeding - covariate	HATCH	Mean hatching date, 1 March = 1
Vole abundance estimates – covariates.	VPHAUT	Voles per hectare, autumn prior to breeding attempt
Values from the assessment site nearest each territory.	VPHSPR	Voles per hectare, spring of breeding attempt
	VPHSUM	Voles per hectare, summer of breeding attempt
	VPHAUT2	Voles per hectare, autumn of dispersal

that survival depends only upon time. Exploratory plots showed that, when sex, brood size or year were used as factor variables, this assumption was invalidated. Therefore, Kaplan-Meier survival analysis was used to examine survival rates.

The Kaplan-Meier method calculates cumulative probability of survival functions based upon the proportion of cases that are still alive at each death "event" by multiplication of individual survival probabilities up to and including that point in time. Pairs of survival distributions (three-chick broods and those of other sizes, males and females, or 1996 and 1997) were compared using the log rank statistic. This is a chi-squared analogue and tests the null hypothesis that two or more survival functions were equal overall. It is based upon the difference between the observed and expected number of deaths at each time point.

Unlike standard regression techniques, Kaplan-Meier analysis allows the inclusion of "censored" data. Cases are censored when they are not known to have died within the observation period (in this case, birds with which contact had been lost). The fact that an individual was alive up to the point of loss of contact is represented in the analysis, because censored cases contribute information to all intervals during which they were observed. Survival probabilities are not estimated at censored times because the proportion surviving does not change at these points. Only the number of cases still under observation is decreased. Thus, this analysis produced results based upon the minimum number of deaths. The time variable used was the number of days lived after fledging, calculated individually for each bird. A set point in real time was not used because deaths occurred before the last chick of each radio tagged group had fledged in both years.

3.2.5 Recruitment and tag effects

During the study period, all nestlings were ringed prior to fledging, and most breeding adults were caught (S.J. Petty). Thus, any recruits into the breeding population were easily recognised. Owls were radio tagged at 22-32 (mean 27.0) days of age, and at 1-11 (mean 5.5, SE 0.3) days before fledging, so that most had time in the nest to grow accustomed to the tags. The combined mass of the tag and harness (chapter 2) represented 1.7 - 4.2% (mean 2.4%) of a juvenile's mass at its last weighing (1-11, mean 4.8, SE 0.3, days before fledging).

Recruitment of individuals from 1996 and 1997 radio tagged (treatment) and non-radio tagged (control) groups into the 1997 and 1998 breeding populations was compared using the 95% confidence interval around the estimate of the proportion of non radio tagged birds which were recruited, calculated as: $\pm = 1.96*(\text{sqrt}(p(1-p)/n))$, where p is the proportion and *n* is the sample size. If the 95% confidence interval around the estimated proportion of untagged birds that were recruited did not include the estimated proportion of tagged birds that were recruited, there was a statistically significant difference between the two recruitment rates and the null hypothesis that they were equal could be rejected. Equal probability of dispersal outside the study area was assumed for both groups. The possibility that rearing conditions differed between control and treatment groups was investigated by comparing start of incubation (where 1 = March 1), clutch size and brood size between broods in the treatment and control groups in both years.

3.3 Results

3.3.1 Data collected

Table 3.3 details the origins and numbers of VSI assessments used in seasonal estimates of vole abundance. Tables 3.4 and 3.5 give the origins and fates of birds in the 1996 and 1997 radio tagged groups respectively.

3.3.2 Food abundance and breeding

3.3.2.1 Food abundance

Field vole density estimates in the nearest estimation sites to nest boxes where broods were radio tagged (*n* sites used for each season = 7-13, mean 12.7) increased in the winter of 1995/1996 from their lowest mean point of 36 animals per hectare in the autumn of 1995 (figure 3.3a). After reaching a mean of 68 animals per hectare in spring 1996, vole numbers fell to around 55 per hectare in summer, and 40 per hectare by autumn. In the winter of 1996/1997, vole densities increased sharply, reaching a mean of 80 animals per hectare by spring 1997 and generally increasing to around 113 per hectare in summer. As in 1996, numbers decreased into the autumn (the independence and dispersal period), when the mean density was 102 animals per hectare.

Table 3.3 *The number of VSI assessments performed in Kielder Forest in 1996 and 1997 by observers C.F. Coles, J.L. MacKinnon, and S.J. Petty. These assessments were available for use in chapters 3-5 inclusive. Additional assessments specific to any one area of the study are detailed in the appropriate chapters. The table also gives the number of assessments used for vole abundance estimates in this chapter (tables 3.6 and 3.7), and details the numbers of sites included where mean values were used.*

Group	ID	Autumn 1995	Spring 1996		Summer 1996	Autumn 1996		Spring 1997	Summer 1997	Autumn 1997	
		n sites	*n* sites	SE voles	*n sites*	*n* sites	SE voles	*n sites*	*n sites*	*n* sites	SE voles
Nest box	T3	1	8	7	1	8	7	1	1	8	11
	T120	-	7	11	1	8	9	N/A	N/A	N/A	N/A
	T144	N/A	N/A	N/A	N/A	8	9	1	1	8	9
	T149	1	9	6	1	12	6	1	1	8	5
Observer	CFC	-	-		26	30		-	73	84	
	JLM	-	137		75	215		31	31	93	
	SJP	20	20		20	20		20	20	20	
	n available	20	157		121	265		51	124	197	
	n used	7	32		11	46		11	13	34	

Table 3.4 *Summary of composition of the 1996 radio tagged group, including gender (data B.M. Appleby), breeding data (S.J. Petty) and radio tracking outcomes.*

Nest box	ID	Sex	Hatched	Fledged	Fate
3	GF36858	F	06/05/96	07/06/96	Dead
3	GF36857	M	07/05/96	06/06/96	Dead
25	GF36870	F	10/05/96	10/06/96	Missing
25	GF36869	M	08/05/96	10/06/96	Missing
30	GF36881	F	02/05/96	03/06/96	Dead
30	GF36882	M	04/05/96	03/06/96	Dead
32	GF36860	M	29/04/96	02/06/96	Missing
32	GF36859	M	30/04/96	01/06/96	Missing
45	GF36868	F	12/05/96	12/06/96	Missing
45	GF36867	M	10/05/96	12/06/96	Dead
55	GF36893	F	19/05/96	20/06/96	Missing
55	GF36894	M	20/05/96	19/06/96	Missing
83	GF36900	F	14/05/96	14/06/96	Dead
83	GF36875	M	12/05/96	14/06/96	Missing
91	GF36892	M	22/05/96	26/06/96	Dead
91	GF62107	M	17/05/96	27/06/96	Dead
120	GF36890	F	02/05/96	06/06/96	Dead
120	GF36861	M	02/05/96	07/06/96	Dead
133	GF36898	F	18/05/96	19/06/96	Dead
133	GF36899	M	22/05/96	21/06/96	Dead
149	GF36883	F	07/05/96	07/06/96	Dead
149	GF36884	M	04/05/96	05/06/96	Missing

Table 3.5 *Summary of composition of the 1997 radio tagged group, including gender (data B.M. Appleby), breeding data (S.J. Petty) and radio tracking outcomes.*

Nest box	ID	Sex	Hatched	Fledged	Fate
3	GF62258	F	23/04/97	26/05/97	Dead
3	GF62259	M	23/04/97	26/05/97	Dead
25	GF62286	F	23/04/97	26/05/97	Dead
25	GF62086	M	19/04/97	27/05/97	Dead
25	GF62085	M	19/04/97	22/05/97	Missing
30	GF62073	F	16/04/97	17/05/97	Missing
30	GF62074	M	16/04/97	17/05/97	Missing
30	GF62075	M	19/04/97	21/05/97	Missing
32	GF62285	F	26/04/97	26/05/97	Missing
32	GF62284	F	22/04/97	24/05/97	Dead
32	GF62084	M	20/04/97	20/05/97	Dead
45	GF62255	M	28/04/97	27/05/97	Dead
45	GF62253	M	24/04/97	27/05/97	Dead
45	GF62254	M	24/04/97	27/05/97	Dead
55	GF46596	F	16/04/97	18/05/97	Missing
55	GF46595	F	18/04/97	17/05/97	Missing
55	GF46597	M	16/04/97	20/05/97	Missing
62	GF82501	M	08/05/97	09/06/97	Dead
83	GF46598	M	18/04/97	20/05/97	Dead
83	GF46600	M	16/04/97	18/05/97	Missing
83	GF46599	M	14/04/97	18/05/97	Missing
87	GF62292	F	18/05/97	22/06/97	Dead
91	GF62282	?	24/04/97	25/05/97	Missing
91	GF62283	M	27/04/97	27/05/97	Left study area
91	GF62053	M	20/04/97	25/05/97	Missing
137	GF62299	F	09/05/97	10/06/97	Dead
137	GF62300	M	14/05/97	12/06/97	Dead
137	GF62298	M	10/05/97	12/06/97	Dead
144	GF62071	F	16/04/97	26/05/97	Dead
144	GF62072	F	16/04/97	21/05/97	Dead
149	GF62145	F	27/04/97	31/05/97	Dead
149	GF62144	F	27/04/97	28/05/97	Dead
149	GF62146	M	29/04/97	31/05/97	Dead

The pattern in vole abundance at 20 sites distributed over the entire study area, and including those used in figure 3.3a, was very similar (figure 3.3b). Mean values were highly correlated (Spearman's Rank correlation coefficient, $r_s = 1.00$, $n = 7$, $P < 0.01$), suggesting that vole density estimates in or near the territories where broods were radio tagged were similar to those of the study area in general. Vole densities in the study area during autumn 1997 were significantly higher than those of autumn 1996 (Wilcoxon Signed Ranks test, $Z = -3.40$, $n = 20$, $P < 0.01$).

Within any one season, vole density estimates were highly variable between radio tagged territories in both years (figure 3.3a, tables 3.6 and 3.7). To examine changes in food supply in territories where broods were radio tagged in consecutive years, field vole density estimates were compared on a seasonal basis. Only vole densities in the autumns of 1996 and 1997 differed significantly (table 3.8). However, the power of some tests was reduced by smaller sample sizes, which were the result of a lack of data for some territories in some seasons.

3.3.2.2 Breeding

55.8% and 83.3% of tawny owl pairs in Kielder Forest attempted to breed in 1996 and 1997 respectively. Mean brood hatching and fledging dates in territories where broods were radio tagged in consecutive years were significantly earlier in 1997 than in 1996 (Wilcoxon Paired Rank tests, $Z = -2.67$, $n = 9$, $P < 0.01$ for both variables) (tables 3.6 and 3.7). There was relatively little within-year variation, with the exception of mean brood hatch dates in 1997 (table 3.6). On average, mean hatching and fledging dates were earlier for broods that fledged three chicks (hatching: mean 54.4, SE 2.6; fledging: mean 86.3, SE 2.5 days after 1 March) than those that fledged less than three (hatching: mean 62.3, SE 7.2; fledging: mean 96.6, SE 6.8 days after 1 March). However, there were only four broods that fledged less than three chicks, and these differences were not statistically significant (Mann-Whitney U tests, hatching: $U = 13.5$, $n = 4,9$, $P = 0.49$; fledging: $U = 9.0$, $n = 4,9$, $P = 0.16$).

Figure 3.3. *Mean vole density estimates in 1996 and 1997, a) throughout the territories where broods were radio tagged (*n *assessment sites = 7-13, mean 12.7), and b) for the whole study area (*n *=20)(S.J. Petty, unpublished data). Points of figure 3.4a are not joined because not all territories were included in all seasonal means. The value for autumn 1996 used data from territories from which birds were tagged in 1997 in addition to those studied in 1996 to reflect vole densities prior to 1997 breeding attempts.*

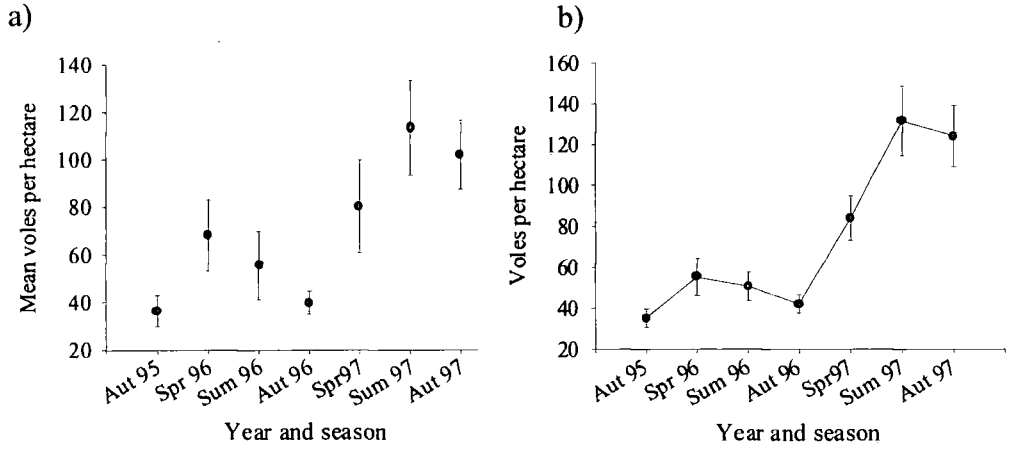


Table 3.6. *Mean clutch hatching (CHD) and brood fledging (BFD) dates (1 = March 1), and seasonal vole density estimates (voles per hectare) for 11 territories where nestling tawny owls were radio tagged in 1996. CVs were used to express variability of data. VSIs were not available for the clear-cut nearest some territories in autumn 1995.Numbers in brackets refer to 1 SE where mean values were used.*

Nest box	Mean CHD	Mean BFD	Autumn 95	Spring 96	Summer 96	Autumn 96
T3	67.0	98.5	63	62(7)	27	77(7)
T25	70.0	102.0	23	102	79	23
T30	64.0	95.0	50	115	105	64
T32	60.5	93.5	50	62	15	37
T45	72.0	104.0	23	102	79	23
T55	80.5	111.5	-	10	15	37
T83	74.0	106.0	-	10	15	37
T91	80.5	118.5	-	10	15	37
T120	63.0	98.5	-	141(11)	156	64(9)
T133	81.0	112.0	23	23	79	37
T149	66.5	98.0	23	115(6)	27	37(6)
Mean	70.8	103.4	23.2	68.4	55.6	43.0
CV (%)	10.5	7.6	48	72	85	41

Table 3.7. *Mean clutch hatching (CHD) and brood fledging (BFD) dates (1 March = 1), and seasonal vole density estimates (voles per hectare) for13 territories where nestling tawny owls were radio tagged in 1997. CVs were used to express variability of data. Data were not available for some territories in every season. Numbers in brackets refer to 1 SE where mean values were used.*

Nest box	Mean CHD	Mean BFD	Autumn 96	Spring 97	Summer 97	Autumn 97
T3	54.0	87.0	77	102	99	64(11)
T25	51.3	86.0	23	23	15	37
T30	48.0	79.3	64	220	113	185
T32	53.7	84.3	37	49	170	171
T45	56.3	87.3	23	23	15	37
T55	47.7	79.3	37	-	43	104
T62	69.0	101.0	23	128	156	118
T83	47.0	79.7	37	10	170	104
T87	79.0	114.0	-	89	85	91
T91	54.7	86.7	37	-	226	104
T137	72.0	103.3	23	75	198	171
T144	47.0	84.5	64	141	156	118(9)
T149	58.7	91.0	37	23	29	23(5)
Mean	56.8	89.5	37.1	67.9	113.5	102.1
CV (%)	18.2	11.7	44	81	64	52

Table 3.8. *Seasonal comparisons of the changes in field vole density estimates in or near tawny owl territories in which broods were radio tagged in both 1996 and 1997 (Wilcoxon Signed Ranks tests).*

Comparison	*n*	Z	P
Autumn 1995 / Autumn 1996	7	-1.76	0.08
Spring 1996 / Spring 1997	8	-0.42	0.67
Summer 1996 / Summer 1997	10	-1.58	0.11
Autumn 1996 / Autumn 1997	10	-2.41	0.02*

3.3.2.3 Relationship between timing of breeding and food abundance

In addition to earlier hatching and fledging in 1997 than in 1996, consistent with the general increase in vole density (section 3.3.1.1), there was a significant negative correlation between mean clutch hatch dates of radio tagged broods and vole abundance in the preceding autumn (Partial correlation controlling for year: coefficient = -0.57, P = 0.07)(figure 3.4, table 3.9). There were no significant partial correlations between mean hatch dates and vole density estimates for spring, summer and the autumn of dispersal (table 3.9).

3.3.3 Radio tagged groups

Both radio tagged groups had male-biased sex ratios (table 3.10). Fledging took place between 29 and 41 (mean 32.4 SE 0.32) days after hatching (table 3.11), with no significant differences in the length of the nestling period between birds when grouped by sex and year, nor any significance of the interaction effect between the two variables (ANOVA model, overall $F_{3,53} = 0.75$, P = 0.53).

Nestling survival was high in the 24 radio tagged broods. In 1996, 22 (88%) of the 25 young that hatched survived to the fledging stage. The figure was similar despite higher modal brood sizes in 1997, when 33 (89%) of 37 hatched young fledged.

3.3.4 Longevity and origin of dead birds

Birds that were found dead lived for 0 to 199 (mean 72.7, SE 10.4) days post-fledging (table 3.12). In 1996, the 13 birds found dead were from eight broods. In 1997, the 20 corpses recovered were of individuals from 10 broods, with three birds found dead of three tagged in three cases, two birds found dead of three tagged in two cases, one bird found dead of three tagged in one case, two birds found dead of two tagged in two cases, and the remaining birds being the only members of their broods to fledge successfully.

3.3.5 Factors affecting juvenile survival

3.3.5.1 General Linear Models

Vole abundance estimates from different seasons were tried in separate models to investigate which provided the best fit. Initial models included the brood size variable and year as categorical covariates, and mean hatching date with combinations of

Figure 3.4. *The relationship between vole density estimates in the autumn prior to breeding, near natal nest boxes where tawny owl broods were radio tagged, and variation in mean clutch hatch dates. Symbols distinguish broods from 1996, and those of modal and less than modal sizes from 1997. One SE bars are shown where mean values were used.*

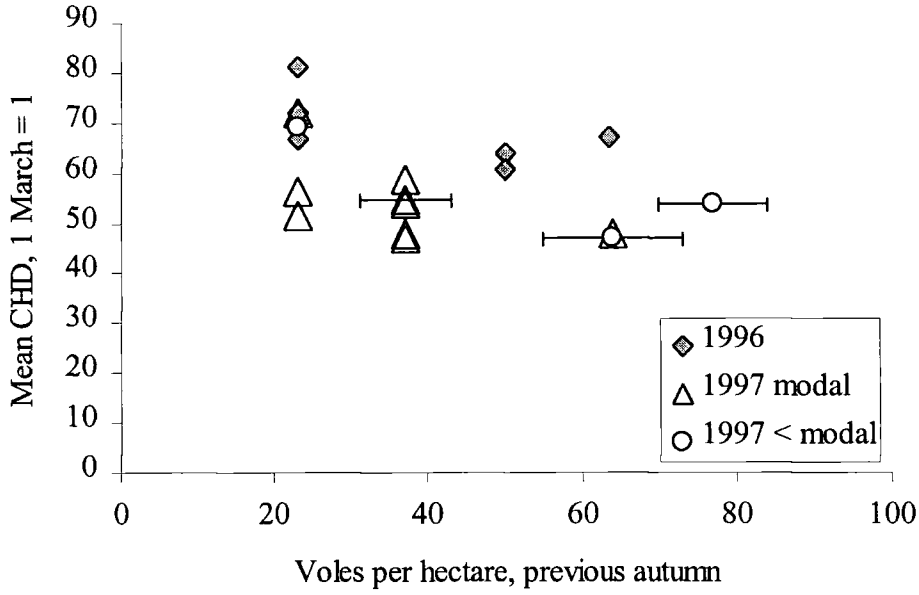


Table 3.9. *Partial correlation matrix of mean clutch hatch dates (CHD) and brood fledging dates (BFD) of tawny owls radio-tagged in 1996 and 1997 with seasonal vole density estimates at sites near natal nest boxes, controlling for the effects of year (df = 14). Vole density variables are: preceding autumn (AUT), spring (SPR), summer (SUM) and autumn of dispersal (AUT2).*

		Voles per hectare			
		AUT	SPR	SUM	AUT2
CHD	Coefficient	-0.56	-0.01	0.20	-0.06
	P	0.02*	0.99	0.47	0.83
BFD	Coefficient	-0.59	0.02	0.21	-0.09
	P	0.03*	0.95	0.44	0.74

Table 3.10. *The numbers of individuals of known sex in the radio tagged groups. Percentages are in parentheses.*

Year	Male	Female	Ratio M:F	Total
1996	13 (59.1)	9 (40.9)	1.44:1	22
1997	19 (59.4)	13 (40.6)	1.46:1	32
Total	32 (59.3)	22 (40.7)	1.45:1	54

Table 3.11. *Known fledging ages (days after hatching) for two groups of radio tagged juvenile tawny owls. In 1997, one bird went missing before it was located outside the nestbox and therefore, its fledging date was unknown.*

Year	Group	*n*	Min	Max	Mean	SE
	Male	13	30	41	33.00	0.39
1996	Female	9	31	35	31.89	0.42
	Total	22	30	41	32.60	0.54
	Male	18	29	35	32.00	0.40
1997	Female	13	29	40	32.90	0.78
	Total	32	29	40	32.31	0.39

Table 3.12 *The number of days lived after fledging for juvenile male and female tawny owls whose remains were recovered in the two study years.*

Group	*n*	Max	Min	Mean	SE
Male	18	199	0	55.89	11.69
Female	15	197	19	92.67	14.23
1996	13	134	8	65.23	11.05
1997	20	199	0	77.40	14.07

vole abundance variables and interaction terms between variables as covariates. Thus, I found that year (P = 0.96), vole abundance in the previous autumn (P = 0.98) and vole abundance in the autumn of dispersal (P = 0.5) were not useful predictors of survivorship. Inclusion of vole abundance in summer (P = 0.10) improved the fit, but the best model explained 55.4% (45.1% adjusted) of variation in days lived ($F_{3,18}$ = 6.15, P = 0.01) and included significant contributions from the following variables: spring vole abundance estimates ($F_{1,18}$ = 5.65, P = 0.03), mean hatch date ($F_{1,18}$ = 7.50, P = 0.02) and whether a modal number of nestlings fledged from the brood to which dead birds belonged ($F_{1,18}$ = 5.56, P = 0.04).

Mean hatching dates was significantly negatively correlated with days lived after fledging (partial *r*, controlling for year *r* = -0.64, *n* = 14, P < 0.01)(figure 3.5), but there was no significant correlation between survivorship and spring vole abundance estimates (partial *r*, controlling for year = 0.37, df = 14, P = 0.16)(figure 3.6). The relationship between survival and brood size is investigated further in section 3.3.5.3.

3.3.5.2 Gender of dead birds

The null hypothesis that there was no difference between the observed frequencies of females found dead in both years, and those predicted from their proportion in the radio tagged study groups could not be rejected (X^2 = 0.18 with Yate's correction, df = 1, P = 0.67)(table 3.13). This infers equal likelihood of death for both sexes, but does not consider missing birds, nor examine the patterns of mortality in relation to time or other influences.

3.3.5.3 Survival rates

A more rigorous analysis looked for differences between paired survival functions and included all radio tagged juveniles. Male and female survival rates were not proportional to one another over time (figure 3.7). However, the null hypothesis that there were no differences between the distributions of days lived after fledging by males and females could not be rejected (Log rank test, X^2 = 0.01, df = 1, P = 0.92)(table 3.14).

Figure 3.5 *The relationship between the mean number of days lived post-fledging (± 1 SE) and mean clutch hatch date for 18 broods of tawny owls from which at least one member was found dead in 1996 and 1997.*

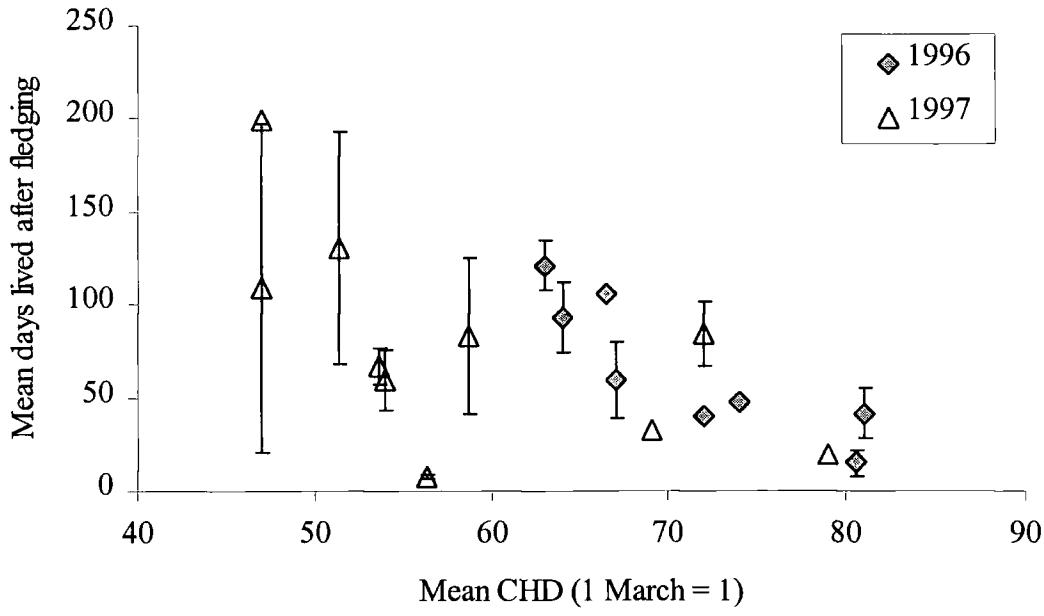


Figure 3.6 *The relationship between the mean number of days lived post-fledging (± 1 SE) and number of voles per hectare near nest boxes in spring (± 1 SE where a mean value from multiple assessment sites was used) for 18 broods of tawny owls from which at least one member was found dead in 1996 and 1997.*

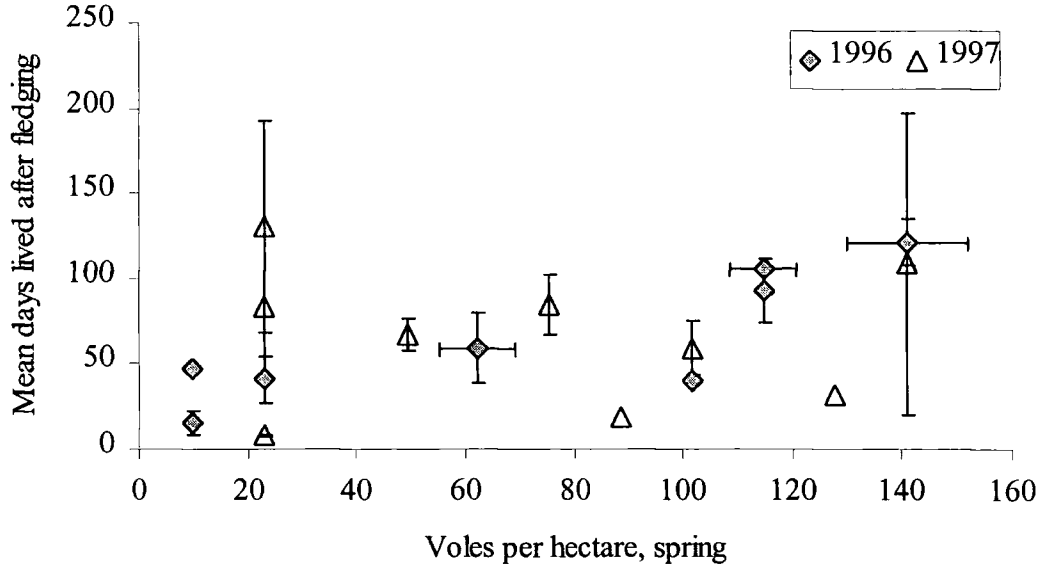


Table 3.13. *The number of female tawny owls found dead (observed) and that expected given their proportion in the radio tagged groups of 1996 and 1997.*

	1996	1997
Observed (found dead)	6	9
Expected (total × proportion of females)	5.32	8.12
Proportion of females (tagged group)	0.41	0.41

Table 3.14. *Summary of juvenile tawny owl survival data. The 1997 group has been broken down by brood size (modal size = 3). A bird of unknown sex was radio tagged in 1997, from a brood of modal size. The days lived column refers to the period for which birds were known to be alive. It includes birds that died and those with which contact was lost without death being recorded ("censored").*

Group	Sex	*n*	Censored		Days lived	
			No.	%	Mean	SE
1996	Male	13	6	46.2	81.1	15.5
	Female	9	3	33.3	85.9	11.6
1997 modal	Male	17	8	47.1	140.7	24.9
	Female	9	4	44.4	192.0	47.5
1997< modal	Male	2	0	0.0	37.5	5.5
	Female	4	0	0.0	77.8	41.9

Year of study was not shown to be a predictor of the number of days lived after fledging (section 3.3.5.1). This was confirmed in a comparison of survival functions for all birds in 1996 and 1997, including data for birds with which contact was lost, which showed no significant statistical difference (Log rank test, $X^2 = 2.07$, df = 1, P = 0.15)(figure 3.9a).

However, the 1997 sample included birds from broods from which less than the modal number of chicks (3) fledged. Birds from these broods died more quickly (mean survival time 64.3 days, SE 27.8, $n = 6$) than those from broods of modal size born in the same year (mean survival time 164.1 days, SE 21.9, $n = 27$)(Log rank test, $X^2 = 6.55$, df = 1, P = 0.01)(table 3.14, figure 3.8) and had a survival function that was statistically similar to that of 1996 birds (Log rank test for difference, $X^2 = 0.87$, df = 1, P = 0.35).

Thus, birds from 1997 broods of less than modal size were omitted from a second paired comparison of yearly survival functions, revealing that the remaining 1997 birds died significantly more slowly than their 1996 counterparts (Log rank test, $X^2 = 4.41$, df = 1, P = 0.04)(figure 3.9 b, table 3.14). After this exclusion, the survival functions of the sexes remained statistically similar (Log rank test, $X^2 = 0.07$, df = 1, P = 0.79). In 1997, three birds were relocated throughout the winter of 1997/98 and into the spring when contact was lost, possibly due to the onset of radio tag failure. One of the censored cases left the study area and the fate of the others remained unknown. The last known deaths were on 8 November in 1996 and 30 November in 1997.

3.3.5.4 Recruitment and tag effects

None of the 1996 cohort was recruited into the breeding population in 1997 (table 3.15). In 1998, eight (9% comprising 3 males and 5 females, all from different broods) non-radio tagged birds were recruited from the 1996 and 1997 cohorts, but no radio tagged birds were recruited from either cohort. The 95% confidence interval (0.20) around the estimated proportion of untagged birds that were recruited (0.09) included that of the tagged birds that were recruited (0). Therefore, the difference between the two recruitment rates was not statistically significant and the null hypothesis that they were equal could not be rejected.

Figure 3.7. *Kaplan-Meier cumulative survival functions plotted for male and female juvenile tawny owls radio tagged in 1996 and 1997.*

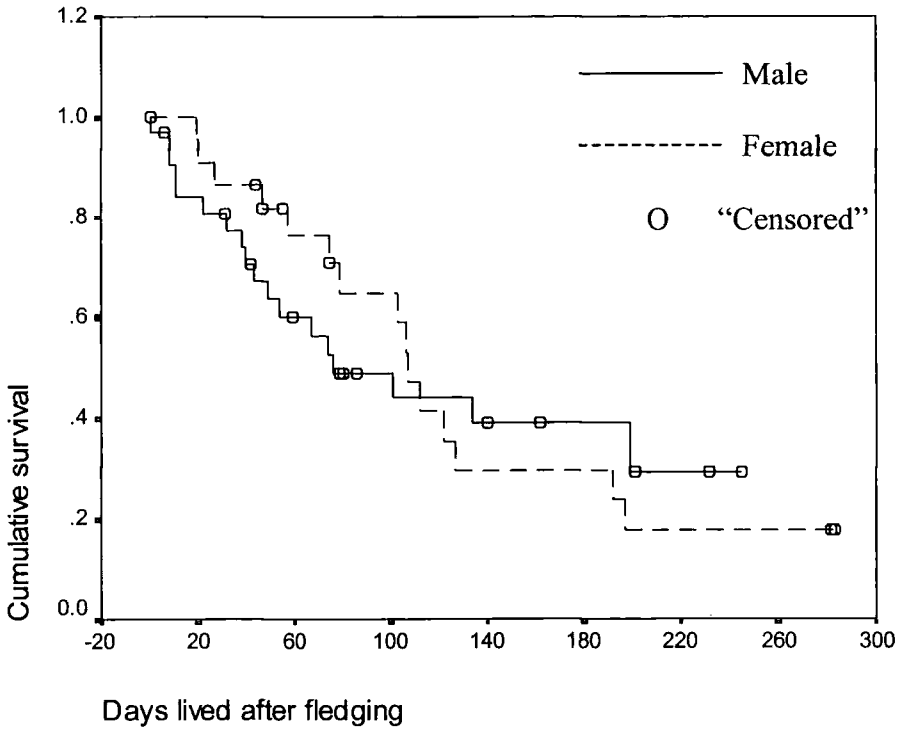


Figure 3.8 *Kaplan-Meier cumulative survival functions plotted for juvenile tawny owls radio tagged in 1997 from broods of modal size (3), and those of less than modal size.*

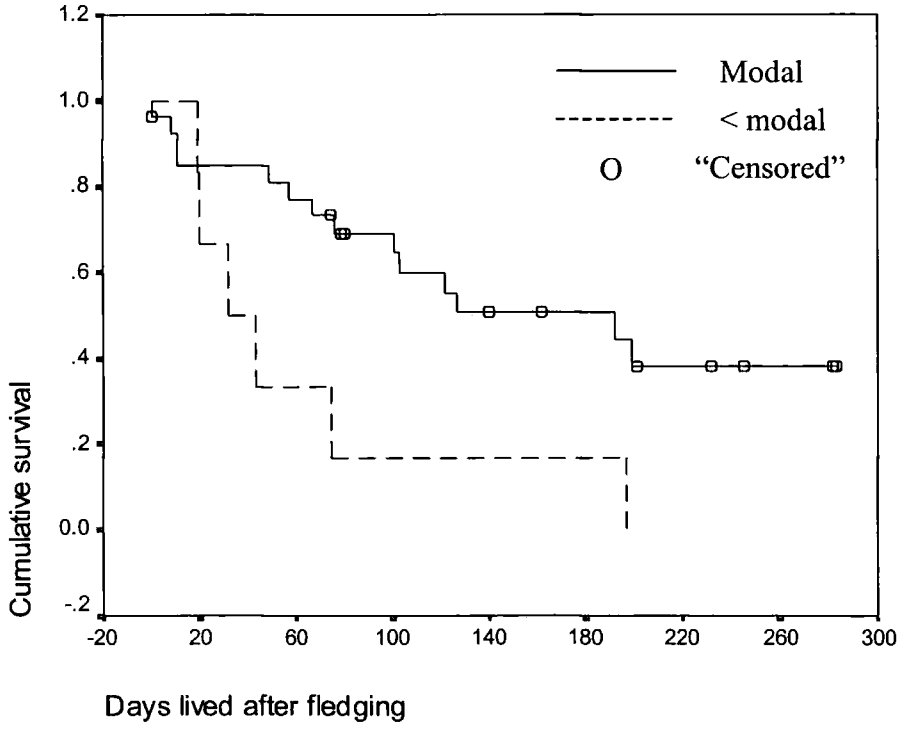
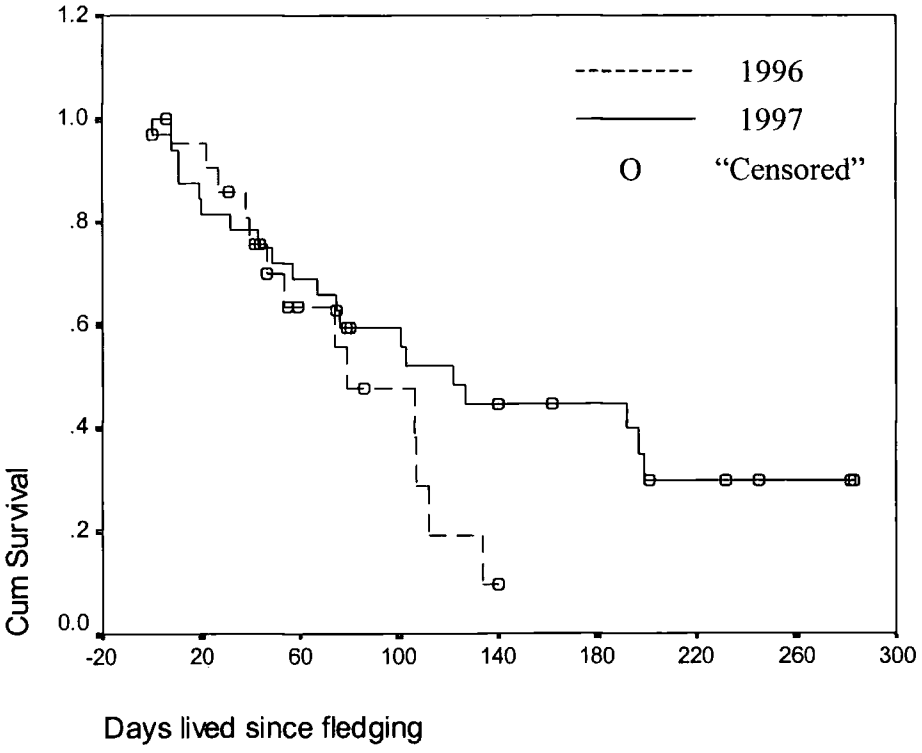


***Figure 3.9**. Pooled sex Kaplan-Meier cumulative survival rate plots of juvenile tawny owls radio tagged in 1996 and 1997, a) including all birds and b) excluding birds from broods from which less than 3 chicks fledged from the 1997 group.*

a)



b)

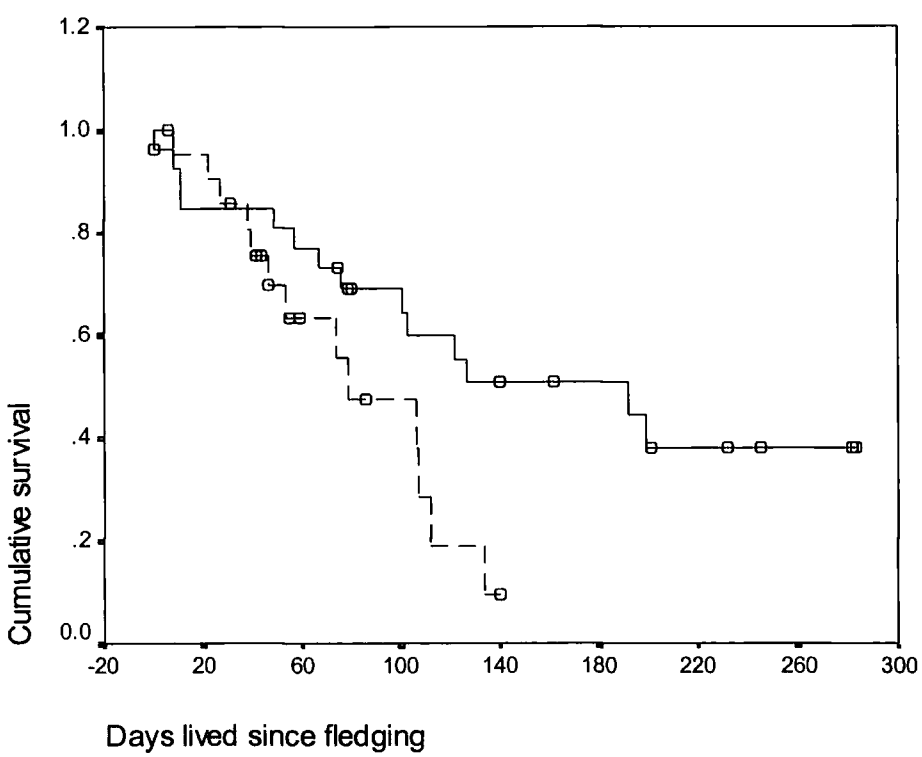


Table 3.15. *Recruitment of radio tagged and non-radio tagged broods of tawny owls ringed in Kielder Forest in 1996 and 1997 into the 1998 breeding population (recruitment data – S.J. Petty).*

Cohort	Radio tagged group			Non-radio tagged group		
	No. ringed	No. recruited	No. broods	No. ringed	No. recruited	No. broods
1996	22	0	11	26	3	14
1997	33	0	13	65	5	26
Total	55	0	24	91	8	40

Table 3.16. *Breeding parameters of radio tagged and non radio tagged tawny owl broods in 1996 and 1997 in Kielder Forest (data - S.J. Petty* et al. *in prep.) Only nests that reared at least one chick are included. Start of incubation was measured as days after 31 February.*

Year	Parameter	Radio tagged			Non radio tagged			Mann-Whitney	
		Mean	SE	*n*	Mean	SE	*n*	U	P
1996	Start of incubation	41.36	2.22	11	41.29	1.62	14	77.0	1.00
	Clutch size	2.27	0.14	11	2.50	0.17	14	63.5	0.38
	Brood size	2.00	0.00	11	1.86	0.14	14	66.0	0.35
1997	Start of incubation	26.31	2.89	13	24.31	1.12	26	162.0	0.83
	Clutch size	3.08	0.21	13	3.08	0.09	26	158.0	0.67
	Brood size	2.54	0.22	13	2.42	0.15	26	150.0	0.52

There were no significant differences in start of incubation, clutch size and brood size in the treatment and control groups in either 1996 or 1997, indicating that the differential recruitment rates could not have been explained by differences in rearing conditions (table 3.16)(Petty *et al.* in prep.).

3.3.4 Timing and causes of mortality

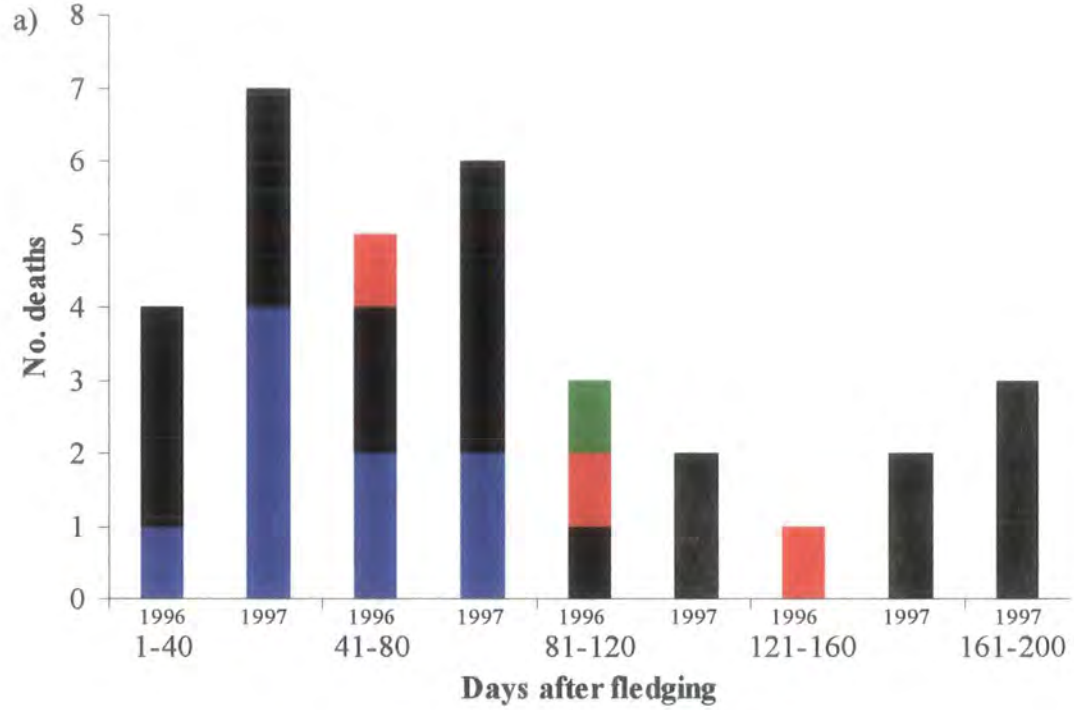
The observation period was divided into five 40-day phases (figure 3.10a). In 1996, the largest number of known deaths occurred at 41 to 80 days after fledging. Three owls were killed by goshawks (*Accipiter gentilis*) before 42 days post-fledging whereas starvation, which accounted for six deaths, occurred throughout the observation period. In 1997, the largest number of known deaths occurred 1-40 days after fledging. No deaths were attributable to predation after 80 days post-fledging, and starvation continued to kill owls throughout the period, similarly to 1996.

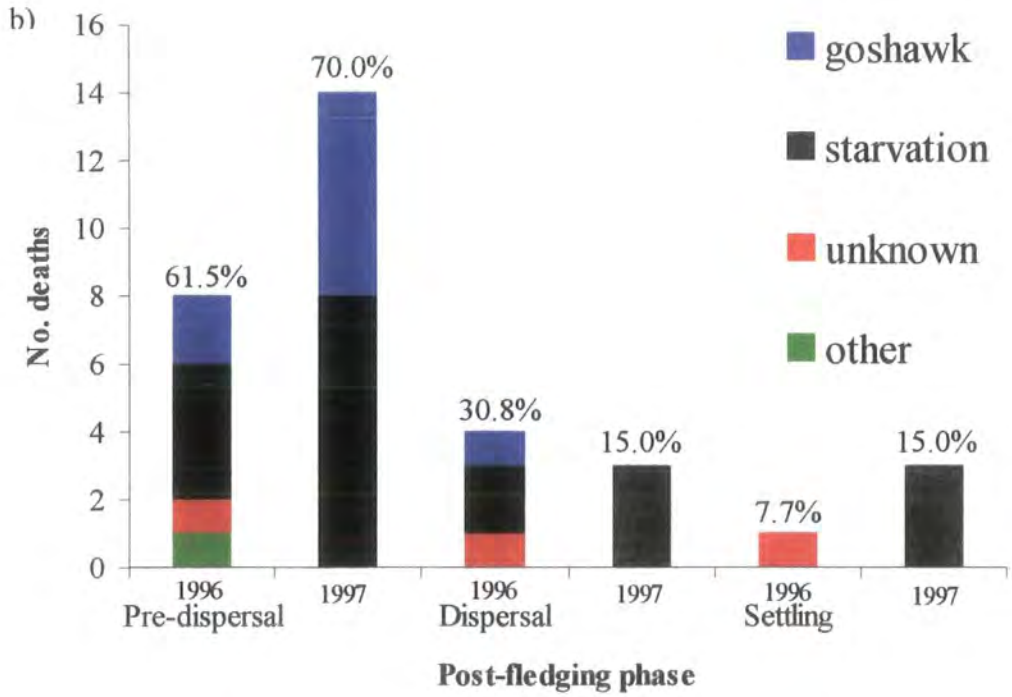
In terms of phases of the post-fledging period that were more biologically meaningful (for definitions of which see chapter 4), more known deaths occurred before the onset of dispersal than afterwards (figure 3.10b). However, statistical analysis showed that this difference was not significant (X^2 with Yates' correction = 0.02, df =1, P = 0.89)(table 3.17).

Table 3.17. *Contingency table to test the null hypothesis that the frequencies of known deaths of juvenile tawny owls radio tagged in 1996 and 1997 did not differ before and after the dispersal period. O = observed frequency, E = expected frequency.*

Period	Year		Total *n*
	1996	1997	
Before dispersal	O = 8, E = 8.67	O = 14, E = 13.33	22
After dispersal	O = 5, E = 4.33	O = 6, E = 6.67	11
Total *n*	13	20	33

Figure 3.10. *Timing and causes of mortality of juvenile tawny owls whose remains were recovered; a) in terms of days after fledging, and b), in terms of phase of post-fledging period, defined individually from the behaviour of each bird (chapter 4). A fatal eye injury to one bird in 1996 was assigned to "other" in the legend.*





In 1996, 46.2% of recovered birds had starved, and 23.1% were killed by goshawks. The respective figures for 1997 were 41.8 and 29.9% Goshawks were the only predator directly responsible for owl deaths for which the cause could be identified. Two corpses found in 1997 had been partly eaten by a fox, but this was after birds were able to fly strongly allowing them to roost high in trees. Examination of their emaciated bodies suggested that starvation was the primary cause of death.

3.4 Discussion

3.4.1 General comments

Unlike Petty (1992), who sought to establish the factors responsible for variation in survival rates over the three-year vole cycle in Kielder Forest, I was presented with two cohorts of radio tagged owls from which every bird either died or became missing. However, there was considerable variation in the timing of these deaths, particularly in the increasing vole year, when three birds survived the winter. Therefore, I sought to identify the inter-relationship of factors responsible for this variation and compare the results for low and increasing vole years. This discussion aims to acknowledge and explore the limitations of the approach I have taken, and to relate my findings to current knowledge of first year survival patterns of avian species.

3.4.2 Prey abundance, prey availability and survival

For reasons outlined in the introduction (section 3.1), the fact that prey abundance is mediated by a variety of factors so that it differs to prey availability and, ultimately, to "food supply" has special relevance to this chapter. However, this important general issue applies throughout this thesis and imposes limitations upon VSI methodology.

VSIs are useful in comparing relative field vole abundance between patches, and the relationship between this index and other density estimates remained robust between sampling sites (Lambin *et al.* 2000). However, the index takes no account of factors associated with prey availability such as weather patterns, habitat differences (such as the total amount of suitable foraging habitat), vegetation structure or prey activity. Thus, in some cases, failure to reject null hypotheses concerning owl biology

in relation to vole abundance may be due to discrepancies between relative abundance and relative availability.

The assumptions made in selection of VSI sites for analyses are another potential source of error. I used only one VSI site to represent vole densities in most territories, and the sampling error associated with single sites is greater than that where an average of multiple sites is used (Lambin *et al.* 2000, chapter 7). However, assigning multiple sites in the absence of any foraging or home range data would not have increased my confidence in the representative quality of estimates, which was the over-riding consideration for selection of sites in this part of my study. It seems reasonable to suppose that adults made at least some use of the nearest suitable foraging site, particularly given the relatively high wing loading of owl species (Earhart and Johnson 1970), and an assumption that birds should not incur travelling costs in excess of any potential benefits to be gained by foraging further away. In addition, chapter 5 suggests that ranging behaviour of territorial owls is at least partly influenced by the minimum distance to a potential hunting site. Without foraging data, however, there would have been rather less justification for having included more distant sites. The sampling errors associated with VSIs are quantified in chapter 2 (table 2.2) and discussed at length in chapter 7. Some issues concerning the definition of profitable foraging habitat and suggestions for possible refinements of such estimates are discussed in chapter 5.

Returning to the question of prey availability, Fernandez *et al.* (1994) showed how forest succession and inter-site habitat variation may interact to affect rodent community composition. In Kielder Forest, the domination of clear-cuts by grasses is aided by roe deer (Petty 1999), which selectively browse broadleaved trees, shrubs and herbs (de Jong *et al.*1995). VSI sampling areas were chosen on surface water gleys dominated by *Deschampsia cespitosa, Agrostis tenuis* and *Juncus effusus* for uniformity. Sites that were made unsuitable for voles due to new tree growth were not used. These measures avoided sampling sites with great variation in prey availability due to differences in vegetation structure. It is worth emphasising that the use of VSIs in Kielder Forest is not novel, and that S.J. Petty (1992, 1999) explained much of the variation he observed in tawny owl fecundity, recruitment and survival using vole abundance estimates measured in this way.

Weather patterns did not differ significantly between study years (chapter 2), but effects of daily patterns could not be measured due to a 24-hour sampling period at the Kielder Castle station. For example, the amount of precipitation over a 24-hour period gives no clue as to when or how intensely it fell. Thus, my personal observations were consistent with Appleby's (1995) findings that adults were less active in heavy rain and wind, but an attempt to quantify this relationship for three males followed continuously in 1998 met with no success. I assumed that within each study group, birds experienced largely similar weather conditions when provisioning broods. Another assumption was that the time available in each day for hunting was similar between broods, and for any one date between years.

Such a study could be improved by collecting radio tracking data to establish exactly where adults were hunting in relation to their broods, and to sample these sites intensively using VSIs or another vole abundance index. Multiplication of vole densities by the area of available foraging habitat would then provide the best possible measure of relative prey abundance, although assumptions would have to be made as to what constituted foraging habitat (also see chapter 5).

3.4.3 Factors affecting "survival"

High levels of mortality in both years mean that the calculation of annual survival rates would have been of limited informative value. However, the analysis of within-year patterns of survivorship was interesting. Petty (1992) showed that between-year variation in timing of breeding by tawny owls in Kielder was correlated with vole densities in the preceding autumn and winter. He also found that an interaction between vole abundance and male experience explained much of the variation in the start of breeding when vole numbers were low, but that breeding experience as a pair (birds which had bred together previously) had the most influence when vole numbers had reached their peak and varied relatively little between territories. My results were consistent with these findings because vole numbers had not peaked by 1997, when the relationship between autumn vole abundance and timing of breeding was still relatively strong. These results also increased my confidence in my vole abundance estimates.

Offspring produced by early breeders can gain a survival advantage (Daan *et al.* 1988, Spear and Nur 1994, Catry *et al.* 1998). For tawny owls in Kielder Forest, such advantages may be that earlier hatched chicks have longer to become efficient hunters before winter, face less severe competition for territories, or avoid the heaviest predation likely to occur during the chick-rearing period of goshawks. To expand upon this last statement, the mean first egg laying date of goshawks in the Border Forests is 16 April (n = 323), and around 5-6 days later in Kielder (S.J. Petty, personal communication). Incubation lasts 35-37 days and chicks start to fledge at around 39 days of age, remaining near to the nest site for a further 2-3 weeks. Thus, the earliest nesting tawny owls (first week in March) fledge chicks around two weeks before goshawks hatch, by which time the young owls will be in the tree canopy and are fairly good fliers. However, the chicks of later breeding birds fledged during the period when foraging effort of breeding adult goshawks presumably increased to provision nestlings. Thus, the presence of predators such as goshawks may further increase the selective advantages of early breeding.

However, the greatest effects of early breeding upon survival are probably due to the nature of early breeders themselves. Parents generally reach breeding condition earlier when food is more abundant (Petty 1992) and this better territorial food supply may then improve the condition of nestlings, conferring a survival advantage. A number of studies have shown positive correlations between post-fledging survival and pre-fledging condition (e.g. Magrath 1991, Gaston 1997, Overskaug *et al.* 1999). Overskaug *et al.* (1999) found that heavier tawny owl nestlings had a greater probability of survival. Indirect evidence from this study supported this idea in that vole abundance during spring (March-May), the period including the fastest and most critical nestling growth, contributed significantly toward explaining variation in survivorship. In 1997, the broods that fledged less than three chicks had been reduced in size by early chick deaths and had effective brood sizes of one and two chicks through much of the nestling period. These were probably the offspring of poorer quality adults, as was evident by their later breeding. First year breeders tend to breed later than more experienced birds, and to occupy poorer quality territories (Petty 1992). Petty (1992) showed that the future chances of recruitment of tawny owls reared in Kielder Forest during low and increasing vole years, such as 1996 and 1997 respectively, were strongly influenced by timing of breeding, and by autumn and

winter food supply after fledging. Korpimäki and Lagerström (1988) also found that the food conditions at the time of dispersal strongly influenced the likelihood of Tengmalm's owls to be recruited into the breeding population. My study only considered food abundance in the natal area, although birds tended to die more quickly in 1996 than in 1997, when vole density estimates were generally higher throughout the study area. This statement carries the caveat that the difference was only statistically significant once the later hatched broods from 1997 had been removed.

Paton *et al.* (1991) found poorer survival in radio-tag bearing female spotted owls. Like the tawny owl, these birds show reversed sexual dimorphism and Caccamise and Hedin (1985) suggested that heavier birds may pay a heavier energetic cost of carrying extra mass burdens due to aerodynamic factors. Earhart and Johnson (1970) pointed out that females are already less manoeuvrable than males due to higher wing loading. However, I could find no evidence that radio tagged juvenile female tawny owls suffered higher mortality rates than males. In fact, female tawny owls increase their body weight considerably just prior to breeding (Hirons *et al.* 1984, Hirons 1985a), and thus may be expected to cope better than males with the relatively small addition of weight represented by the attachment of a radio tag.

Back-mounted radio tags are often used in preference to tail mounts, which are liable to cause premature feather moult (Kenward 1987). Previous studies of the consequences of radio attachment to owls have reached no firm conclusion, some having demonstrated negative effects (Paton *et al.* 1991, Foster *et al.* 1992) and another none at all (Taylor 1991). This was the first study to examine the impact of radio tags on juvenile owls where a control group of non-radio tagged owls has been used, even though radio tagging young owls is commonplace. None of the radio tagged birds in this study was recruited, in comparison to 9% of the control group, and this difference was cause for concern, even if not statistically significant. Similarly, only one of 56 Northern spotted owls tagged in dispersal studies ever paired, and even then, it never bred (Verner *et al.* 1992). Tags may adversely affect energy budgets, increasing the likelihood of starvation, and vulnerability to predation. Therefore, I suggest that great consideration be given to radio tagging the young of any species of *Strix* owl.

Starvation has been highlighted as an important cause of mortality in juvenile tawny owls (Hirons *et al.* 1979, Petty and Thirgood 1989). Hirons *et al.* (1979) stated that the inability to secure a territory reduces their chances of surviving and breeding, which is consistent with the observation that starvation continued to kill owls in Kielder Forest up to and including the settling period. An important indirect effect of food supply has been identified as an interaction with predation risk. Rohner and Hunter (1996) suggested that food shortage increased vulnerability of fledgling great horned owls to predation and was likely to have caused mortality over and above that attributed to starvation. They postulated that the slow development associated with extended parental care may incur costs in terms of susceptibility to mortality under environmental stress (Rohner and Hunter 1996). After recently leaving the nest, tawny owls spend some time on the ground (Petty and Thirgood 1989, Overskaug *et al.* 1999, personal observation) making them vulnerable to predators (Petty and Thirgood 1989). At this time, they are entirely dependent on the defence responses of adults, which increase in very good food years (Wallin 1997, S.J. Petty, personal communication). However, I found no evidence that a smaller proportion of birds was killed by predation as food abundance generally increased from 1996 to 1997.

The trend in some owl species for mortality to peak before, not after, the onset of dispersal (Petty and Thirgood 1989, Rohner and Hunter 1996, Overskaug *et al.* 1999) was not statistically significant in this study. However, my observations were still inconsistent with earlier work from Wytham, which suggested that very few deaths (1.7% of fledglings) occurred before independence (Southern 1970). One explanation for this difference may be that Southern located birds by their calls. This method may have been less accurate than individual marking, despite claims of certainty that all young were traced. An alternative, more likely, explanation is that predation was an important factor in all the studies except the Wytham work, and tended to kill birds earlier on, when they are more vulnerable (see above).

This study suggested that the number of individuals that were recruited into the breeding population was much lower than those that fledged successfully or began to disperse. Thus, recruitment rates may not only be a desirable way in which to measure reproductive success (Spear and Nur 1994), but also may also be preferable

to the use of radio tagging in survival studies, at least for species similar to the tawny owl, and until the effects of attachments are known. This is particularly the case in an environment such as Kielder, given the extremely low recruitment rates in all but one phase of the vole cycle (Petty 1992), even without additional factors. In Wytham, a lowland broadleaved woodland in southern England, juvenile mortality was found to be low, and Hirons *et al.* (1979) stated that predation was unlikely to be an important mortality factor for the tawny owl. Kielder Forest has been colonised by goshawks relatively recently (chapter 1, section 1.2.2), which may have profound effects upon the dynamics of what was previously a relatively stable (e.g. Petty 1992) tawny owl population.

3.5 Summary

Juvenile survival can be viewed as an alternative measure of reproductive success. Previous work has suggested that food supply can affect juvenile survival directly or indirectly via a complex suite of factors. This study of two cohorts of juvenile tawny owls took place during a low vole year (1996) and an increasing vole year (1997). I examined some factors that may have explained the variation that I found in mortality patterns both within and between years.

In territories where broods were radio tagged in consecutive years (9 of a total of 14), breeding occurred earlier in 1997 than in 1996. Mean clutch hatching dates were significantly negatively correlated with vole abundance estimates near respective nest boxes in the previous autumn. Modal brood sizes were two in 1996, and three in 1997. Nestling survival was high in both years at 88 and 89% in 1996 and 1997 respectively, and fledging occurred at 32.4 days of age, on average. There was little deviation from this mean figure, either between sexes or between years. In 1997, four of the radio tagged broods fledged less than three chicks. These broods tended to hatch later than those that fledged three chicks. Vole densities in the study area were significantly higher during the dispersal period (autumn) of 1997 than of 1996.

55.4% of the variation in the mean number of days survived post-fledging by broods from which at least one juvenile was known to have died was explained by a model comprising the variables "mean clutch hatch date", "modal versus less than modal brood size" and "voles per hectare at the clear-cut nearest natal nest boxes in

the spring of breeding". Mean clutch hatch date was significantly negatively correlated with longevity. As well as the inferred inherent higher quality offspring of earlier breeders, a number of additional advantages of this strategy are suggested.

Birds born in 1997 generally lived longer than those born in 1996, when food abundance was generally lower. Juveniles from 1997 broods that fledged less than three chicks died significantly sooner than those from broods that fledged three chicks. When the former group was excluded, survival functions for 1996 and 1997 differed statistically. Males and females were equally likely to die (be found dead), and suffered statistically similar mortality rates.

No member of either tagged group was recruited into the 1997 or 1998 breeding population, whereas 9% of untagged control groups of the same cohorts were recruited, with possible implications for future use of back-mounted radio tags on young *Strix* owls.

In each year, more birds were found dead before the onset of dispersal than afterwards, but these differences were not statistically significant. Mortality was mainly due to starvation and predation. Goshawks were responsible for all confirmed deaths that were directly attributable to predation, which became less important after dispersal. Starvation killed juveniles throughout both monitoring periods. A similar proportion of deaths were attributable to hawks in both years and, thus, there was no evidence that food supply interacted with predation in this study.

VSI methodology has limitations, the chief one being its imperfect representation of food availability as opposed to relative abundance. These limitations are explored with reference to brood provisioning and chick condition.

Due to the possibly detrimental effects of radio tagging and the small number of recruits compared to fledglings, I suggest that recruitment rates may be the preferable way to measure survival patterns and breeding success in populations such as this one. Comparison of my results with work undertaken in lowland broadleaved woodland implies that the dynamics of tawny owl populations may differ according

to predation pressure, which has not been identified as an important mortality factor in such habitats.

Chapter 4 The role of food supply in the dispersal behaviour of juvenile tawny owls

4.1 Introduction

Natal dispersal, an animals' movement from its place of birth to its first breeding site, can have important consequences for populations. Work on natal dispersal has centred on its relative costs and benefits as an alternative strategy to philopatry (e.g. Greenwood 1980). Thus, most authors have asked questions related to the starting and end points - why do animals disperse, and why do some sections of populations move further than others?

Proximate causes of dispersal suggested include demand for nest sites, demand for food, ectoparasite load, physiological switches, intraspecific aggression, avoidance of juveniles, and avoidance of adult conspecifics (summarised by Holekamp 1986). Ultimate causes are regarded as mate competition, inbreeding avoidance, and resource limitation (summarised by Byrom and Krebs 1999).

Of environmental influences, competition for local resources has long been assumed to cause individuals to move further in years of high population, or of low food supply (Lack 1954). In general, the worse the conditions in the area of birth, the greater the advantage of leaving it (Newton and Marquiss 1983). Kenward *et al.* (in press) suggested that buzzards making transitional movements, including post-natal dispersal, were primed by social and environmental factors to travel far. The factors that enhanced movements changed over time, but generally related to the abundance of feeding habitat, and social factors such as the presence of conspecifics. In a Swedish population of tawny owls, both environmental and genetic factors influenced natal dispersal distance and individual fitness (Wallin *et al.*1988). The former included the spatial variation in mean small mammal density among five trapping sites located in a diagonal across the study area. Petty (1992) also highlighted the importance of food supply to dispersing juvenile tawny owls. In both low and increasing vole years, juveniles experienced increasing or high vole abundance during their first winter, in contrast with decreasing vole years where vole numbers had already started to crash by the time the chicks fledged.

Sonerud *et al.* (1988) showed that Tengmalm's owls dispersed further during the microtine peak. However, Korpimäki and Lagerström (1988) found no effect of prey densities upon dispersal distances in a study of the same species. At the scale of individual territories, great horned owls appeared to concentrate their foraging effort on prey "hot spots", although non-territorial floaters showed no tendency to move toward these experimentally elevated prey densities (Rohner and Krebs 1998). However, nomadic owl species exhibit numerical responses to high prey densities at a larger scale (e.g. Village 1987, Korpimäki and Norrdahl 1991).

Viswanathan *et al.* (1999) suggested that the success of random searches could be optimised by varying flight lengths so that long flights became increasingly rare as food densities at "target sites" increased, thus restricting the area covered during foraging. Applied to juveniles moving through the forest, this theory predicts that birds would have made relatively more smaller movements over a given time period in the increasing vole year than in the low vole year

In autumn, during the time of juvenile dispersal, tawny owls become highly vocal and vigorously defend their territories with "song", threatening behaviour and flying skirmishes (e.g. Mikkola 1983). Thus, the presence of territorial birds, and associated risks, may be another factor influencing non-territorial birds as they move through the forest.

The decision process that guides an individual to stay or leave a particular territory should be the core in a theory of dispersal (Wallin *et al.* 1988). The causes and consequences of dispersal have received much attention, but little is known of the influences acting at the level of the decisions made during the dispersal process itself.

My hypothesis is that dispersal behaviour of juvenile tawny owls was influenced by spatial variation in field vole abundance. I set out to test the following predictions:

1. Smaller movements would be relatively more common in 1997, when voles were generally more abundant, so that birds performed a kind of area restricted search.
2. Juveniles would seek to avoid potentially dangerous interactions with territorial adults by avoiding roosting in occupied territories.

3. The length of time that owls spent in any one area was dependent upon vole abundance there.
4. Time spent in areas would also tend to increase with time after dispersal as birds had moved away from natal territories, thus reducing the risk of inbreeding, and began to settle.

In this chapter, the term "dispersal" is used to represent movement away from the nest site and does not necessarily infer that birds were moving away from conspecifics.

4.2 Methods

4.2.1 Prey abundance

In addition to the assessments detailed in chapter 3 (table 3.3), S. Smart performed 16 VSI assessments in the summer of 1997, and S.D. Twiss performed 11 assessments during the winter of 1997/98. These assessments were performed to provide coverage of previously unsampled areas where juveniles roosted. Most of these assessments were on clear-cut patches, but any suitable habitat of at least 0.25 ha was used. This included grassy wayleaves and unplanted streamsides. Vole density estimates were then calculated from indices using the appropriate seasonal formulae (chapter 2).

4.2.2 Radio telemetry

A detailed account of the numbers and distribution of birds radio tagged, fieldwork protocol, determination of fledging date, and sampling frequencies before and after the onset of dispersal is given in chapter 3 (section 3.2.3). All radiolocations of dispersing juveniles were of daytime roosts.

4.2.3 Definitions of phases of the post-fledging period

I refer to the period between departure from the nestbox (fledging) and the onset of dispersal as the pre-dispersal phase. Juveniles sometimes made "exploratory" movements in which they roosted outside the natal territory. However, dispersal soon followed such movements, and I follow Belthoff and Richison (1989) in defining the beginning of dispersal as the date of initial departure. In the absence of direct data, territorial boundaries were largely inferred. Joining the points that lay half the

distance between the nestbox in question and the nestboxes of each adjoining (with no territories in between) territory created Thiessen-type polygons - my best estimate of each "natal territory". In two cases in 1996, and three cases in 1997, I used nocturnal calling positions of radio tagged adults to give a more accurate picture of whether roosting positions of their offspring lay outside their territorial boundaries.

Defining the end of dispersal was problematic, since several birds "settled" in an area for over two months before making a large movement and "settling" elsewhere. A bird was considered to have settled if it remained near the same vole abundance assessment site, or group of sites, for four weeks or more. Birds that moved and then settled again were said to have resettled. These distinctions do not imply the end of dispersal, which, by definition, occurs with a breeding attempt, and none of the radio tagged birds was known to breed (chapter 3).

4.2.4 Movements

4.2.4.1 Summarising movements

The shortest linear distance between the natal nest box and the last known position of each bird was termed the Euclidian distance. The sum total of all distances between successive radiolocations were calculated for illustrative purposes and termed minimum total distances. These were less than the absolute distance moved because owls were not monitored continuously.

4.2.4.2 Between year comparison of movement patterns

Distances moved by birds in 1996 and 1997 were compared by selecting fixes taken over a standardised sampling interval of two days. These were placed into forty 250m classes, ranging from 0 to 10 kilometres, and the frequency of movements in each class was calculated for each year group. The resulting frequency distributions were then compared statistically. Frequencies were arcsinh transformed and a MANOVA (multivariate analysis of variance) model was used to test the hypothesis that relatively higher field vole densities in the areas used by different birds gave steeper regression slopes, as birds restricted their search areas and larger movements became progressively rarer.

4.2.5 Distribution of roosting positions in relation to occupied territories

The Euclidian distance to the nearest occupied nest box (occupancy data from S.J. Petty) was calculated for each fix of dispersing juveniles, and for an identical number (n = 354) of random X,Y co-ordinates. The latter were generated using the RANDBETWEEN command in Microsoft Excel, with the limits of the study area as "top" and "bottom" integers. The two resulting frequency distributions were grouped into twenty-six 250m categories, ranging from 0 to 6.5 kilometres, and compared statistically. A MANOVA model was used with arcsinh transformed frequencies to test for significant differences between slopes. Distance to the nearest occupied nest box was also used as a covariate in the staying time analysis below.

4.2.6 Staying times

4.2.6.1 Definitions of movements and stays

Movements, and "stays" between movements, were defined assuming that roosting birds obtained food in the nearest available habitat suitable for VSI assessment (please refer to chapter 2 for definitions of suitability), and using the following rules:

1. A movement occurred when a bird moved its roosting position so that it was nearer to a different clear-cut or similar area of habitat suitable for VSI assessment (see 3 below).
2. A stay constituted the period between two movements.
3. VSI assessments were undertaken at the nearest suitable habitat patch to the roosting position. Movements of roosting positions to stands of trees that were not bordered on at least one side by habitat suitable for assessment were excluded from the analysis. That there was no area suitable for assessment did not mean that there were no voles in that area. This rule eliminated the subjectivity inherent in the use of distance cut-offs in the absence of foraging data. Such exclusions occurred when roosting plantations were bordered by "unsuitable" habitat such as advanced pre-thicket stage crops, moorland, farmland or water features.
3. The period immediately before death or disappearance was excluded - this "stay" was artificially truncated by the loss of the bird.
5. One VSI assessment was performed per estimated 0.25ha, based upon the minimum area required for the technique to be employed, of the designated patch. Multiple scores were averaged.
6. VSI scores were assigned to areas on a monthly basis, that is, the month in which

the bird visited the area. If the "stay" lasted more than one month, another assessment was performed and a mean value was used.

Henceforth, an "area" shall be defined as the vicinity of an owl roost, or series of roosts, plus the designated VSI assessment patch.

4.2.6.2 General linear models

SPSS GLM was used to construct Type III general linear models to explain variation in staying time. The distribution of residual values was inspected to assess the appropriateness of the model. At the beginning, that is first fix, of each stay, the distance to the nearest occupied tawny owl nest box was recorded, along with the number of days since the onset of dispersal, and error was calculated by counting the number of days since the last location. Error was also recorded in these terms at the end of each stay. Other variables considered were estimated vole density in the area, year of study and individual identity. All variables are defined in table 4.1.

4.3 Results

4.3.1 Data obtained

The number of VSI assessments performed in 1996 and 1997 is detailed in chapter 3 (table 3.3), and in section 4.2.1 of this chapter. Of the 61 vole abundance estimates used for comparison with staying times (see below), 13 were mean values from multiple sites. The variations in estimates between these sites are represented by error bars in the appropriate figures. A total of 1347 juvenile roosting positions were recorded (chapter 2, section 2.2.2.2), and of these, 354 were obtained after the onset of dispersal. Sampling frequencies are detailed in chapter 3 (section 3.2.3).

4.3.2 Characteristics of dispersal

4.3.2.1 The pre-dispersal period

Mean vole densities at 20 sites throughout the study area during autumn were significantly higher in 1997, at 124.3 (SE 15.1) animals per hectare, than in 1996 when numbers averaged 42.0 (SE 4.5) animals per hectare (Wilcoxon Signed Ranks test, $Z = -3.40$, $n = 20$, $P < 0.01$)(S.J. Petty, unpublished data). Chapter 3 (section 3.3.2.1) gives a more detailed account of trends in field vole numbers during 1996 and 1997, both in the study area and in each territory where chicks were radio tagged.

Table 4.1 *Variables considered in GLM models to predict "staying time" in roosting areas (please refer to text for definitions) for radio tagged juvenile tawny owls that dispersed in 1996 and 1997. The method of error calculation is also given.*

Category	Variable	Description
Independent (response) variable	STAY	Length of stay in days. Errors defined by time to fixes before and after each stay
Categorical covariates	YEAR	Year of study – 1996 (1) or 1997 (2)
	BIRD	Individual. Birds were numbered 1-26.
Covariates	DAY	Days since onset of dispersal at first fix of stay. Error defined by time to previous fix.
	VOLES	Estimated vole density at nearest suitable VSI assessment site, or sites, adjacent to roosting plantation.
	BOX	Distance (m) to nearest occupied tawny owl nest box, first fix of stay.

Table 4.2 *Examples of "premature dispersal" in juvenile tawny owls radio tagged in 1996. Distances are Euclidian and "timing" (days after fledging) refers to the onset of dispersal. "Days survived" refers to the numbers of days the bird was known to be alive after beginning to disperse.*

Identity	Timing, days	Distance reached, km	Days survived	Fate
GF36899	21	1.64	29	Starved
GF36875	39	2.63	(20)	Missing
GF36900	40	2.38	13	Killed by goshawk
GF36860	40	0.75	(36)	Missing

Fledging took place between at around 32 days from hatching (chapter 3, section 3.3.3). Nine (40.1% of birds tagged) birds reached the dispersal stage in 1996, and 17 (51.5%) in 1997. Dispersal occurred 21-128 (mean 79.5, SE 4.57) days after fledging, with no difference between years or sexes, nor significant interaction between the two variables (ANOVA model, overall $F_{3,26}$, = 1.02, P = 0.40).

In 1996, several birds dispersed prematurely (table 4.2). These times were much earlier than 90 days, which is often quoted as the period after which fledgling tawny owls become independent (e.g. Southern 1970). These birds either perished or went missing, but two survived for over four weeks.

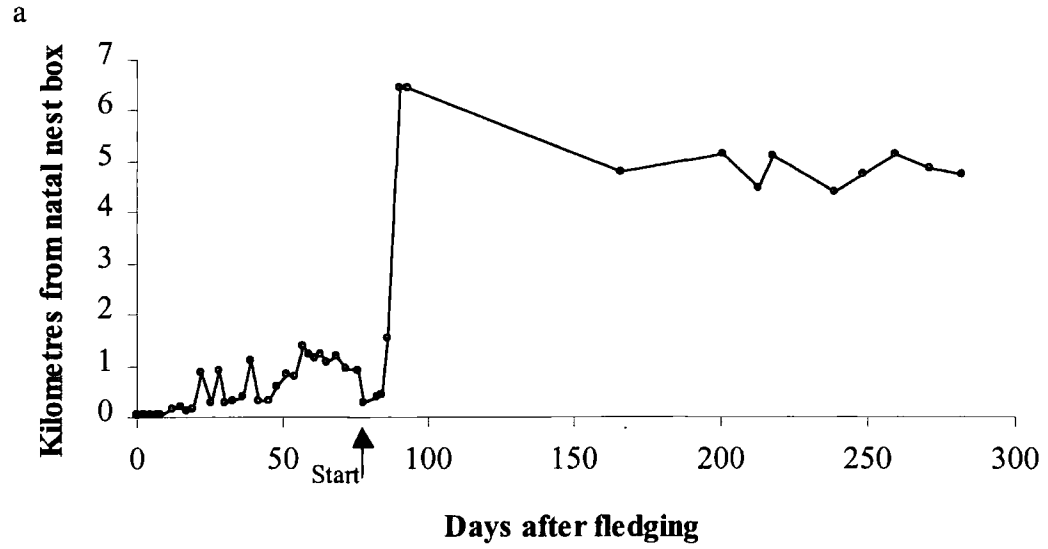
4.3.2.2 Summary of movement and settling patterns

Behaviour varied widely between birds, with some dispersing over a relatively short period, and others settling periodically before moving to a new settling area (figure 4.1). For example, bird GF46596 (figure 4.1a) made its largest dispersal movements over a relatively short period, whereas bird GF46595 (figure 4.1b) settled for 48 days before moving out of the forest. Contact was lost for a short period until it was relocated in the forest, 6.1km from its natal nest box.

Anecdotal evidence showed that dispersing juveniles probably traversed large physical features. Bird GF62053 was located on opposite sides of Kielder Water reservoir on consecutive days, the inference being that it crossed the open water (a linear distance of 1 km) rather than making a much longer trip following the shore (around 16 km). Bird GF46595, which visited a farm outside the forest boundary, was recorded roosting in a plantation near the forest edge at an altitude of 360m. Most birds dispersed in a southerly or south-westerly direction. This was consistent with the orientation of the main valley, and with remaining within the forest boundary.

Two birds from the 1996 group and ten from the 1997 group settled in one area for four weeks or more. Their last known locations were 0.78-6.19 km (mean 3.41, SE, 0.52) from their respective natal nest boxes (figure 4.2), and in this relatively small sample, distances did not differ for males and females (Mann-Whitney test, U = 11.00, n = 7,5, P = 0.29). After leaving natal territories, birds moved minimum total distances of 0.78-82.28 (mean 14.31, SE 3.52) kilometres. Although not corrected for

Figure 4.1. *The timing of dispersal and distance from natal nest boxes over time for two juvenile tawny owls from the 1997 radio tagged group; a) female GF46596, and b) female GF46595. The beginning of dispersal is indicated by an arrow on the* x-*axis.*



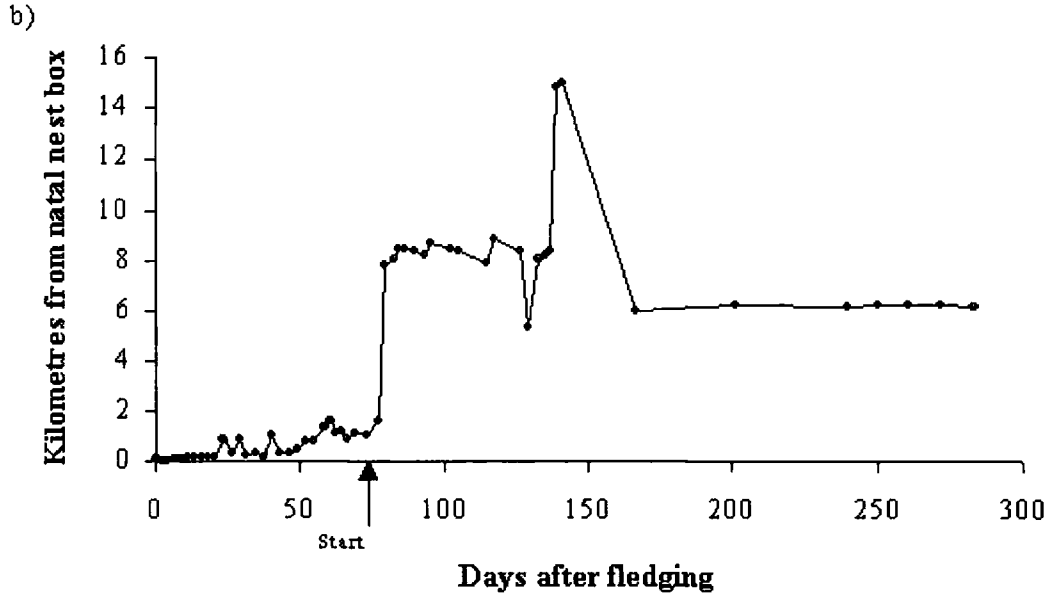


Figure 4.2. *Final radiolocations of 12 juvenile tawny owls that settled in an area for at least one month in 1996 (open circles) and 1997 (filled circles), in relation to the positions of their natal nestboxes (open triangles = 1996, filled triangles = 1997). Dotted lines linking two birds with one nestbox were used in one case to improve clarity.*

the number of fixes, these estimates illustrate how some birds moved much further than could be deduced from the Euclidian distance from their natal nestbox to their final known location (figure 4.3).

4.3.2.3 Between year comparison of movement patterns

In 1996, juveniles moved 0.01-4.05 (n = 76, mean 0.47, median 0.16, SE 0.06) kilometres between fixes taken at two-day intervals. In 1997, birds travelled 0.01-10.00 (n = 74, mean 0.88, median 0.42, SE 0.12) kilometres over the same sampling period. There was no statistically significant difference between the two categorised frequency distributions (Kolmogorov-Smirnov Z = 0.45, n = 80, P = 0.98)(figure 4.4a), and the intercepts and slopes of regressions fitted to the two groups of transformed data were similar (MANOVA, slopes: $F_{1,76} = 0.00$, P = 0.98; intercepts: $F_{1,77} = 2.22$, P = 0.14)(figure 4.4b). Therefore, the hypothesis that smaller movements were more common than larger ones in 1997, when food abundance generally increased, was rejected.

4.3.2.4 Distribution of roosting positions in relation to conspecifics

Prior to dispersal, siblings often roosted close to one another, but after the onset of dispersal, juveniles were rarely found in close proximity. However, in 1996, two birds from different broods roosted in the same stand of trees between two large clear-cut patches in the Bull Crag area for 21 days, until one bird was found dead. It is also likely that territorial adult tawny owls used these clear-cuts because they were surrounded by several occupied territories. Juveniles roosted in the territories of resident adult owls as a matter of course, sometimes for months at a time.

In fact, juveniles roosted 0.01-5.13 (mean 0.98, SE 0.07) kilometres from the nearest occupied nest box, in comparison with a similar number (n =354) of randomly generated co-ordinates, which were 0.07-6.33 (mean 1.68, SE 0.11) kilometres from the nearest occupied box. The two categorised frequency distributions were statistically different, with juvenile fixes being significantly nearer occupied boxes than those created randomly (Kolmogorov-Smirnov Z = 1.40, n = 52, P = 0.04)(figure 4.5a). In addition, the regression slope of transformed data for fixes was significantly steeper than that of random co-ordinates (MANOVA, slopes: $F_{1,48}$ = 15.52, P <0.01)(figure 4.5b). The relationship between juvenile movements and the

Figure 4.3. *Minimum (uncorrected for the number of fixes) total and Euclidian distances travelled by 26 juvenile tawny owls which dispersed in 1996 and 1997, arranged in rank order by minimum total distance.*

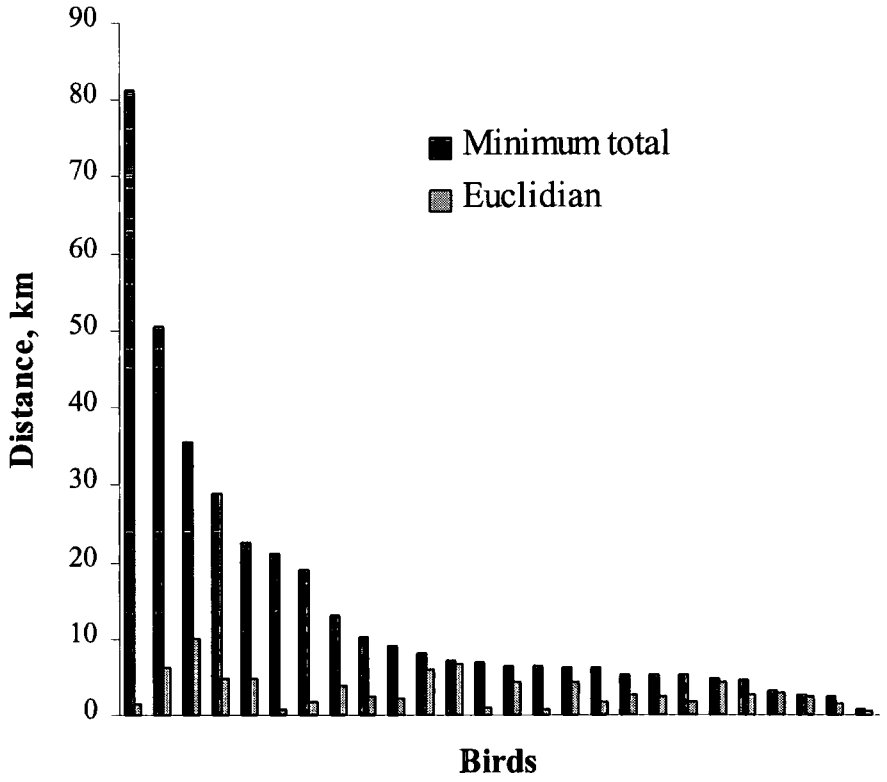


Figure 4.4 *The distances moved between fixes at sampling interval of two days for juvenile tawny owls after the onset of dispersal in 1996 (*n *movements = 76) and 1997 (*n *movements = 74): a) frequency distribution, and b) transformed data.*

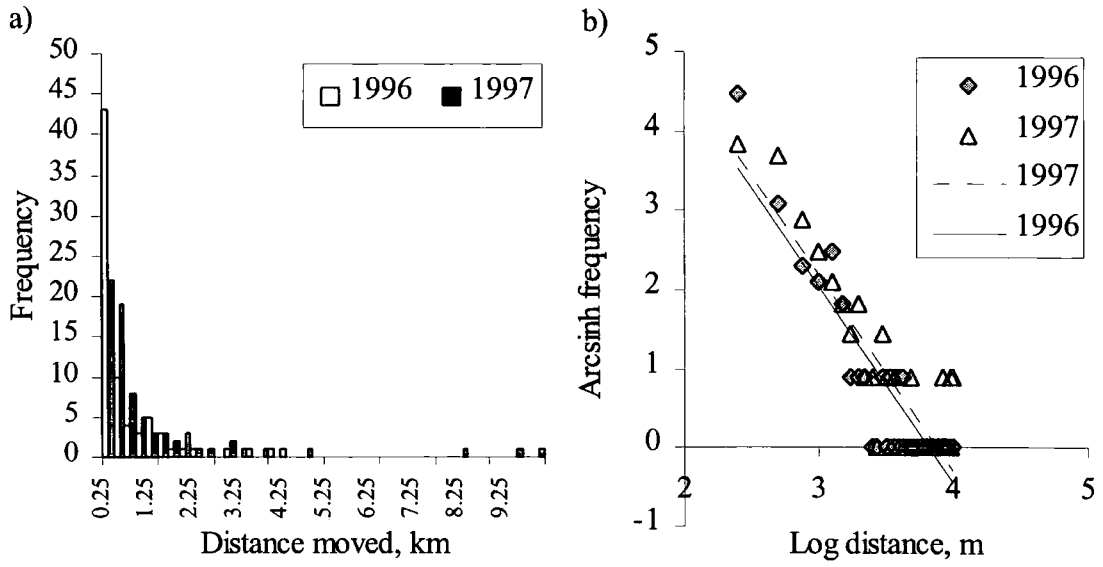


Figure 4.5. *The distances of roosting sites of dispersing juvenile tawny owls in 1996 (118 fixes on nine birds), and 1997 (236 fixes on 17 birds) from the nearest occupied nest box.*

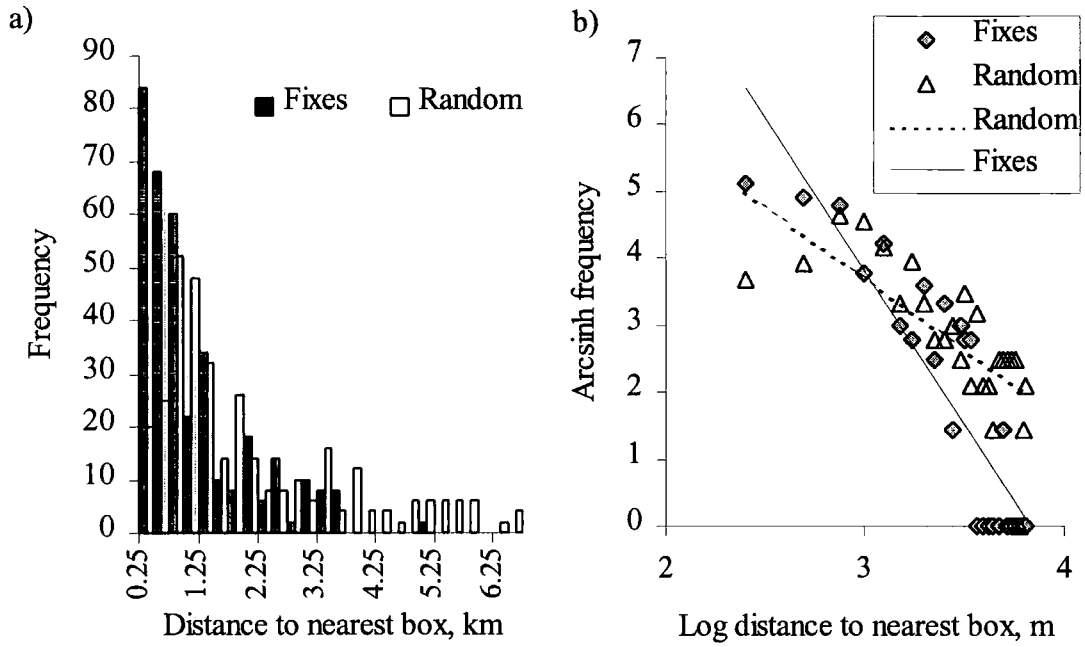


Table 4.3. *Summary of data associated with 61 stays in roosting areas by dispersing juvenile tawny owls in 1996 (*n *stays = 19,* n *birds = 9) and 1997 (*n *stays = 42,* n *birds = 17), which were used in GLM analyses.*

Variable	Year	Min	Max	Mean	SE	CV (%)
Stay length, days	1996	2	45	11.8	2.6	94.9
	1997	2	79	19.7	3.2	106.6
No. stays per bird	1996	1	4	2.1	0.4	61.9
	1997	1	7	2.6	0.4	61.5
Days since dispersal	1996	1	74	17.8	4.2	103.4
(beginning of stay)	1997	2	190	57.1	8.3	93.9
Distance to nearest occupied	1996	29	3822	639.8	205.0	139.7
nest box (beginning of stay)	1997	18	4345	588.9	137.6	151.4
Voles per hectare, nearest	1996	23	229	83.3	13.3	69.4
patch	1997	23	252	114.7	9.6	54.3

location of territorial adults was explored further by considering the distance to the nearest occupied nest box as a possible covariate of the time that juveniles spent in different areas (see below).

4.3.3 Staying times

4.3.3.1 GLM models

Sixty-one discrete periods spent by juvenile owls in any one "area" were identified. Data associated with these stays are summarised in table 4.3.Vole abundance estimates in staying areas tended to be higher in 1997 than in 1996, although this difference was not statistically significant (t = -1.86, df = 59, P = 0.07) and the level of variation was similar (homogeneity of variance, F_{max} = 1.16, df = 1.16, P = 0.38).

All variables (table 4.1), plus interaction terms for year of study with vole abundance, and year with days since dispersal, were included in a GLM model. This was not statistically significant ($F_{29,60}$ = 1.54, P = 0.12), and, therefore, the variables "individual" (P = 0.47), days since onset of dispersal (P = 0.65) and "year by day number" interaction (P = 0.72) were excluded from consideration as useful predictors of stay length at this stage.

Vole abundance was the best predictor in the initial model (P = 0.01) and, therefore, this variable was used as a basis to which others were added in an attempt to improve the model fit. Vole abundance alone accounted for 25.7% (24.4 adjusted) of the variation in staying time ($F_{1,60}$ = 20.41, P < 0.01). Combining year of study ($F_{1,60}$ = 0.50, P = 0.46), distance to nearest occupied nest box ($F_{1,60}$ = 0.53, P = 0.53) or a year by vole abundance interaction ($F_{1,60}$ = 0.49, P = 0.49) with vole abundance all contributed less than a further one percent to the variation explained by respective models.

4.3.3.2 Relationships between variables

Relationships between the variables considered in the GLM models were explored to investigate possibilities such as correlations between vole abundance in staying areas and time after dispersal, or length of stay and year. A partial correlation matrix

Figure 4.6 *Relationship between vole abundance estimates at staying areas (± 1 SE where mean values were used) of dispersing juvenile tawny owls in 1996 and 1997 and the number of days stayed (errors: + days before next fix; – days elapsed after previous fix).*

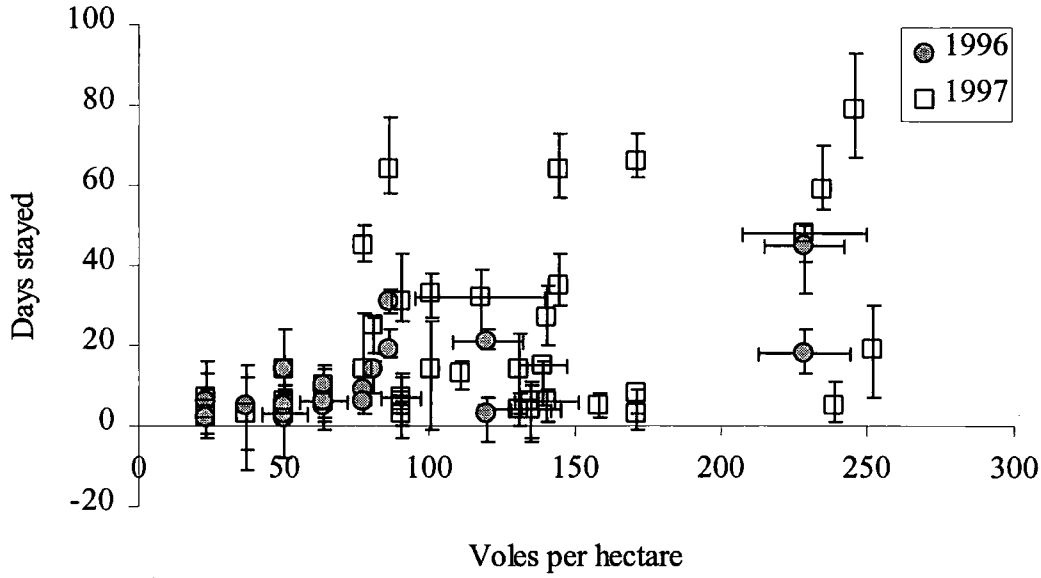


Table 4.4 *Matrix of partial correlations (df = 58), controlling for year of study, between variables used in GLM models to explain variation in staying times for juvenile tawny owls radio tagged in 1996 and 1997. Variables are defined in table 4.1.*

Variable	STAY		DAY		VOLES	
	r	P	*r*	P	*r*	P
STAY	-	-				
DAY	0.08	0.52	-	-		
VOLES	0.48	<0.01**	0.01	0.96	-	-
BOX	0.14	0.30	0.07	0.59	0.12	0.68

Table 4.5 *Matrix of partial correlations (df = 58), controlling for vole abundance, between variables used in GLM models to explain variation in staying times for juvenile tawny owls radio tagged in 1996 and 1997. Variables are defined in table 4.1.*

Variable	STAY		DAY		BOX	
	r	P	*r*	P	*r*	P
STAY	-	-				
DAY	0.12	0.36	-	-		
BOX	0.08	0.52	0.05	0.73	-	-
YEAR	0.09	0.48	0.36	<0.01**	-0.05	0.68

Figure 4.7 *Vole abundance estimates at staying areas of dispersing juvenile tawny owls in 1996 and 1997 in relation to the timing of the stay with reference to the onset of dispersal. X axis error bars, in days, were due to differences in sampling frequency. Timing after dispersal was measured on the first day of each stay and, therefore, these errors were negative only. Y error bars relate to variation between sites where mean VSI scores were used in estimates.*

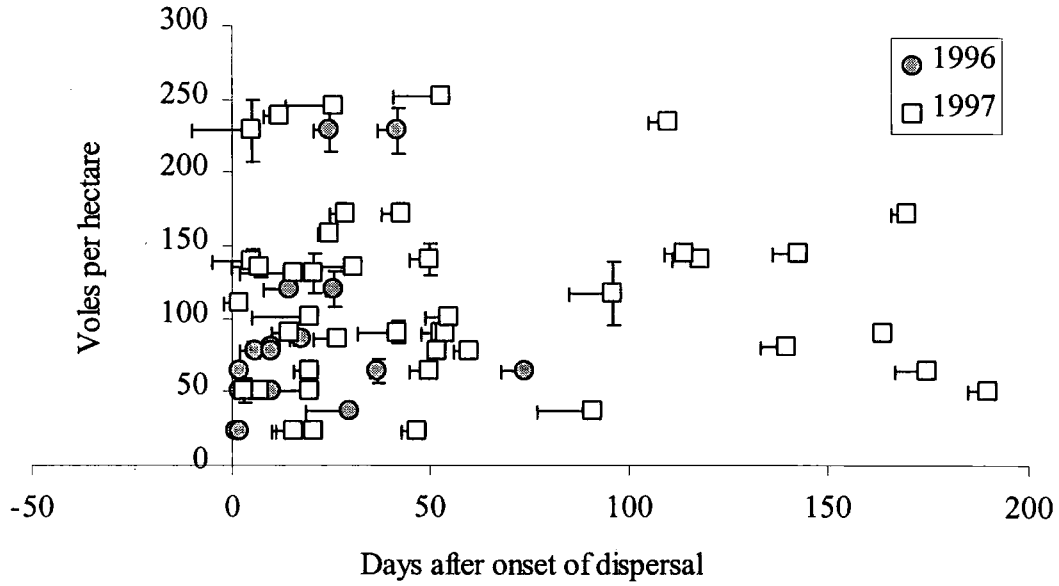
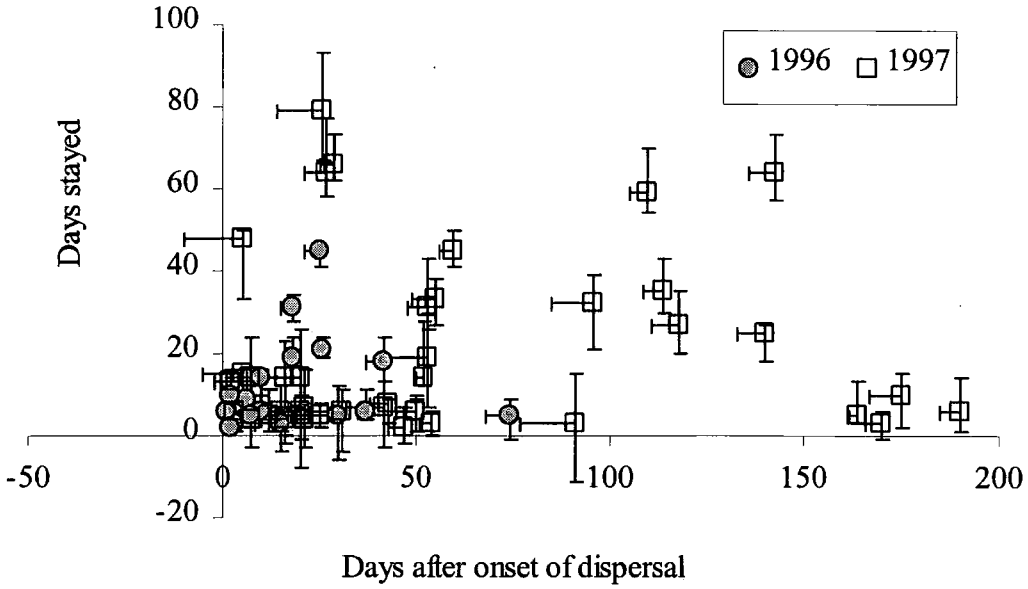


Figure 4.8 *The length of stays made by dispersing juvenile tawny owls in 1996 and 1997 in relation to the timing of the stay with reference to the onset of dispersal. Errors are in days and were due to differences in sampling frequency. Timing after dispersal was measured on the first day of each stay and, therefore,* x *axis error bars are negative only.*



was constructed, controlling for year. Only vole abundance was significantly correlated with stay length (figure 4.6), and there were no significant correlations between any of the other variables (table 4.4). A second analysis, controlling for vole abundance, revealed a significant correlation between year of study and days since onset of dispersal (table 4.5), consistent with the tendency for birds to survive longer in 1997. Again, there were no other significant correlations. These results confirmed that neither vole abundance nor stay length tended to increase with time since dispersal (figures 4.7 and 4.8). Bird identity was omitted from these analyses because it was a categorical variable. Any correlation between the numbers assigned to individuals and other variables would have been coincidental.

4.4 Discussion

4.4.1 Characteristics of dispersal

The average post-fledging period in this study was consistent with previous findings of around 90 days (Southern 1970) and 81 days (one individual, Petty and Thirgood 1989). However, in 1996, three birds moved away from their birthplace before half this average duration had elapsed. Low prey densities are thought to postpone dispersal (Ferrer 1992, Rohner and Hunter 1996), possibly by slowing the development required to reach a critical stage in development necessary for dispersal (Rohner and Hunter 1996). However, Southern *et al.* (1954) stated that nocturnal movements of fledged young tended to oscillate out toward the edge of the known parental territory and back to the centre. If juveniles roosted where they happened to be at daybreak, it is possible that I have misinterpreted a steady movement toward the outer boundaries of large adult feeding ranges (chapter 5) as the onset of dispersal.

Alternatively, hunger may have forced these birds into attempting to support themselves, although dependent juveniles are thought to make little or no effort to feed themselves (Southern *et al.* 1954). The significance of the extended post-fledging period in some species is poorly understood, and there seems scope for more work to determine at what point juveniles begin to hunt, and whether independence necessarily coincides with the onset of dispersal. Certainly, it would be advantageous for hunting skills to have developed well before moving away from the natal territory.

I did not attempt to identify the "end" of dispersal, given that none of the radio tagged groups was known to have survived to breed. In addition, birds that had apparently settled made extensive movements after roosting in the same area for extended periods.

4.4.2 Dispersal as a foraging behaviour

Assuming that there are no restrictions on movement, such as physical barriers or exclusion by other individuals, dispersing birds are free to search for optimal habitat and adequate food supplies. On the first point, Kielder Water reservoir and the hills surrounding the study area did not seem to curtail dispersal movements, although my evidence was purely anecdotal.

Secondly, the nocturnal nature of owls confers the advantage that, if they are silent, their presence may go undetected by territorial birds. Non-territorial great horned owls were silent, ranged more than territorial birds, and had ranges that overlapped defended territories (Rohner 1996). I could not confirm whether dispersing tawny owls were silent, as calls from plantations during darkness could not be attributed to any one bird. However, the presence of territorial owls did not seem to discourage dispersers from remaining in areas for substantial periods. Only once were two dispersing birds assumed to be using the same feeding patch, but that they did so for three weeks may suggest that their choice of roost site was not affected by the presence of conspecifics. In addition, the distribution of roost sites in relation to occupied nest boxes did not suggest avoidance of such territories. In fact, juveniles roosted significantly nearer to territory holders than expected from random. This may be because birds tended to occupy low ground in valley bottoms, where both clear-cuts and tawny owl nest boxes were mainly confined (Petty 1992). Random fixes, however, were distributed throughout the forest, included areas where feeding resources were sparse.

I assumed that juveniles foraged near to where they roosted. Work on the energetics of kestrels by Masman *et al.* (1986) underlined the crucial role of foraging in the energy budget, since it determines both the gross energy intake and a large part of the energy expenditure. Therefore, it seems reasonable to suppose that an animal would not spend time and energy in flights to and from a distant feeding site,

avoiding suitable resources existing nearby. However, the true nature of nocturnal interactions between birds at feeding patches is unlikely to be revealed without simultaneous telemetry data from a number of individuals (also see chapter 5). I also acknowledge that my results may have been affected if juveniles foraged in areas other than those where prey abundance was estimated. I envisage that this may have been a particular problem where owls had a choice of feeding sites nearby, with relatively little difference between travelling distances.

Recent theoretical work has recognised the fact that foragers have limited information available to them, and may take advantage of cues in their local environment to lead them to areas that are more favourable (Grünbaum 1999). If the behaviour of dispersing owls was a larger scale analogy of foraging behaviour, it would have conformed to some, or all, of my predictions. The first was that owls would make relatively more large movements in 1996 when an adequate food supply was harder to find. This was not the case for movements at a given sampling frequency. The variability of vole density estimates in the areas visited was similar in both years, even though vole numbers in the study area were generally higher in 1997. Therefore, the difficulty in discriminating the best patches may have been similar in both 1996 and 1997. The overall distance moved by birds in this study was not compared due to variation in longevity and sampling frequency. Sonerud *et al.* (1988) and Wallin *et al.* (1988) have shown effects of cyclic variations in food supply upon natal dispersal distances in Tengmalm's owls and tawny owls respectively. None of the birds in this study was later recruited (chapter 3) and so no comparison could be made.

The prediction that owls would settle for longer in areas where estimates of prey abundance were higher, was confirmed. It must be stressed that single VSI values are prone to error, and that these give a best estimate of relative abundance. Grass clippings take a varying amount of time to decay, depending upon the season (Lambin *et al.* 2000) but, generally, the index is not useful in detecting changes in density over a timescale shorter than approximately one month (J.L. MacKinnon, personal communication). Most stays were of less than one month and, therefore, I could not confirm whether birds left when patches had been depleted. Thus, there is potential for further work on the economics of staying in an area rather than leaving

in it, and when it becomes profitable to do so. Intensive small mammal trapping in areas used by dispersing owls may reveal changes in prey abundance in the shorter term, and thus be used to investigate whether owls tend to leave an area once prey densities fell below a certain threshold - that is, the point at which an area was no longer adequate in terms of prey availability. It would also be desirable to quantify predation rates, and the number of owls using each area.

Given the imperfect knowledge an organism has of its environment, it was to be expected that vole densities would not increase in successive areas visited (measured as time since dispersal). Rather, relatively low vole densities were associated with shorter stays so that, although owls could not choose from unknown areas, they reacted to those that they did experience. No evidence suggested that birds became relatively more sedentary with time since the onset of dispersal. However, in addition to the need to find sufficient food, birds may react to pressures that prevent them from remaining near their natal area, or near siblings (Kenward *et al.* in press), such as inbreeding avoidance (e.g. Greenwood 1980). The estimation of time since dispersal was prone to sampling error, which may at least partly explain the lack of such a pattern in this study. In addition, several juveniles starved to death (chapter 3) and were clearly under food stress for at least a proportion of the time since they began to disperse. This may have altered their behaviour so that finding food sources became the over-riding factor in determining their movements.

In conclusion, I suggest that food abundance may influence dispersal decisions to some extent in the short term, even though the wider process may be governed largely by other factors.

4.5 Summary

This chapter investigated the effects of food supply upon decisions made by dispersing juvenile tawny owls in 1996 and 1997, two years of contrasting field vole abundance.

The mean length of the pre-dispersal period was around 80 days in both years. The "premature dispersal" of four birds in 1996 at 23-40 days post-fledging may have

been an artefact caused by movement of roosting positions within large parental home ranges, or a response to food stress.

Radio-telemetry revealed more of the true extent of dispersal movements of juvenile tawny owls than Euclidian distances between birthplaces and final radiolocations did. A mean minimum total distance of 14.31 kilometres was covered, uncorrected for the number of fixes, with one individual travelling at least 82.28 kilometres in total. The distances moved between fixes taken two days apart did not confirm the prediction that birds would cover more ground per movement in 1996, when searching for less abundant food. On average, the final locations of 12 birds that settled in an area for four weeks or more were 3.41 kilometres (Euclidian distance) from their birthplaces. Since none of the radio tagged birds was found breeding in the study area, and birds would sometimes settle for a relatively long period before moving again, it was not possible to identify the end of natal dispersal *per se*.

Juveniles roosted nearer to occupied nest boxes than was expected at random. This was possibly because occupied nest boxes and the grassy clear-cuts that juveniles were assumed to be using both tended to be located along valley bottoms. In addition, the time that they spent in different areas was not related to their distance from the nearest occupied nest box.

Owls had an imperfect knowledge of the environment and responded to variability in estimated field vole densities by altering the time spent in different areas rather than by moving to areas with successively greater vole densities. Vole abundance alone explained 25.7% of the variation in the time spent in different areas. Mean vole densities in the areas visited were 83 and 115 animals per hectare in 1996 and 1997 respectively.

There was no detectable decrease in the tendency to move as time elapsed, although the detection of movements was prone to error. This study is consistent with other recent work that has suggested that, although dispersal may be initiated by a variety of proximate and ultimate factors, individual decisions made during dispersal

may depend at least partly upon environmental conditions encountered during the process itself.

Chapter 5 Habitat selection and home range characteristics in relation to field vole abundance and the distribution of foraging habitat.

5.1 Introduction

The relationship between dispersion of individuals within populations of species and the distribution of key resources is central to behavioural ecology, population ecology and conservation biology. For example, information concerning space use and habitat choices of spotted owls in commercial forests has allowed investigators to develop demographic models and habitat management guidelines (e.g. Carey *et al.* 1990, Solis and Gutiérrez 1990, Call *et al.* 1992, Carey *et al.* 1992, Forsman *et al.* 1996, Gutiérrez *et al.* 1998).

Habitat type is an indicator of productivity and has been used to predict differences in red fox *Vulpes vulpes* population density and, by inference, home range size (MacDonald *et al.* 1981, Harris and Rayner 1986). However, differences in productivity alone may not explain why home range sizes vary at a given site (Geffen *et al.* 1992). The home ranges of some carnivores seem to correlate with the distribution of key habitat, leading to the general proposal that the dispersion of food patches determine territory size - the resource dispersion hypothesis (RDH, MacDonald 1983). From the RDH, it is predicted that home ranges are configured to encompass areas where prey are abundant, without reference to those where they are not. Thus, home ranges should encompass similar areas of fruitful habitats in terms of food supply, but widely different areas of useless ones, so that home ranges would be larger where fruitful patches are fragmented and highly dispersed (Geffen *et al.* 1992).

Unlike nomadic raptors that specialise on microtine prey, such as European kestrels *Falco tinnunculus* (Village 1982) and short-eared owls *Asio flammeus* (Village 1987), tawny owls are sedentary birds that often defend a territory for life (Hirons 1976). However, contrary to the traditional assumption that resident tawny owls carry out most of their activities within territorial boundaries (Southern and Lowe 1968, Southern 1970, Galeotti 1994), a recent study has shown that home ranges of the tawny owl in a lowland broadleaved woodland overlapped, and often differed markedly from the defended area (Appleby 1995). The possibility that tawny

owls used areas outside those that were defended was also suggested by Redpath (1995) in a study of a population inhabiting continuous fragmented woodland.

Home range and territory sizes of raptors and owls have been shown to vary with landscape characteristics (Southern 1970, Hardy 1992, Galeotti 1994, Carey and Peeler 1995, Redpath 1995) social characteristics (Galeotti 1994) and food density and dispersion (Lockie 1955, Kenward 1982,Village 1982, 1987, Carey and Peeler 1995, Zabel *et al.* 1995).

In Kielder Forest, the landscape was characterised by large, relatively homogeneous stands of coniferous trees of a variety of ages, punctuated with grassy clear-cuts where field vole abundance was highly variable in time and space. Increasing population density of tawny owls was related to increasing structural diversity of the forest habitat in terms of edge length (Petty 1989). In addition, the birds also seemed to avoid nesting on higher ground, despite availability of nesting habitat and nest boxes in such areas (Petty 1992). Several tawny owl territories may adjoin a clear-cut, so that these patches represent shared food resources, with implications for the pattern of range dispersion. Newton (1979) suggested that the progression from an exclusive range, in which an individual (or pair) has sole use of food sources, to a nesting colony, where only a small area around the nest is used exclusively, represents a series of adjustments to increasingly widely-spaced and sporadic food resources.

With reference to the relationship between spacing behaviour and feeding requirements, I ask how space use of tawny owls in Kielder was related to that of conspecifics, to the distribution of foraging habitat, and to patterns of field vole abundance. More specifically:

1. Was the habitat composition of the study area representative of that of the forest?
2. Did the habitat composition of the area familiar to owls differ from that of:
    i) The study area
    ii) The immediate environment, defined as the watershed in which territories were located.
3. How did home range characteristics vary in relation to:

i) Sex of bird.

ii) Year.

iii) Locality.

iv) The amount of habitat suitable for voles and lengths of habitat edges included.

v) Field vole abundance and dispersion.

5.2 Methods

5.2.1 Fieldwork protocol

In 1996 and 1997, eight (four pairs), and seven (two pairs, two breeding males, one non-breeding male) adult tawny owls were radio tagged, respectively. Four pairs of tawny owls, of which two were studied in both years, had territories in the Deadwater Burn valley system. Three male birds studied in 1997 had territories in the Kielder Burn valley system. These valleys were located in the north of the study area and were tributaries of the river North Tyne before it widened into Bakethin Reservoir (figure 5.1).

Birds were radio-tracked from July (1996) and June (1997) until November (both years). Locations of birds during the nestling period, when they were closely associated with nestboxes, were not included in home range estimates. I collected a maximum of two fixes per bird per night, taken at intervals of three hours or more apart. The activity patterns of tawny owls vary over the course of a night (Mikkola 1983, Appleby 1995). Therefore, the order in which birds were located was changed nightly so that over the tracking period, data for each part of the night had an equal chance of inclusion in individual home ranges. Sample sizes were insufficient to describe home ranges separately before and after the post-fledging dependence period of young and, therefore, home ranges in 1996 and 1997 represented an average for breeding and post-breeding periods. An additional three males were radio tagged in 1998 and followed continuously for periods of 2 to 7.5 hours during May and June of that year.

5.2.2 Temporal autocorrelation and the time to independence

Autocorrelation of positional data occurs when the position of an animal at "time t + change in t" is not independent of its position at time t; thus autocorrelation enables

prediction of an animal's location based on its last position (Rooney *et al.* 1998). Highly correlated data can result in under-estimates of home range size (Swilhart and Slade 1985) and erroneous descriptions of range utilisation (Cresswell and Smith 1992).

Therefore, curves of distance from roost over time (Redpath 1995) were drawn for the three owls radio tagged in 1998. Each was monitored continuously from leaving its roost at dusk until returning to it at dawn (that is, for one full night). The time to statistical independence (the shortest time interval between two non-correlated data points) was taken at 100 minutes, where the mean curve first levelled (figure 5.2). However, the variation between birds was large and, statistically, any point from approximately 80 to 160 minutes may have been chosen. The three continuous data sets were sub-sampled randomly at intervals of at least 100 minutes in order to extract statistically independent data for incorporation into home range estimates using parametric techniques. This produced one to four (mean 2.2) fixes per tracking session, a similar value to that obtained for birds tracked in 1996 and 1997.

5.2.3 Habitat selection

5.2.3.1 Land cover classes

A copy of the Forestry Commission's Kielder Forest GIS database was made, and programs were written to reclassify land uses and tree crops in sub-compartments into 14 classes likely to be discriminated by tawny owls. These classes were termed habitat types, in the same sense as the "habitats" referred to by Aebischer *et al.* (1993) when describing the compositional analysis technique. Their habitat use terminology is adopted throughout this chapter. The forest database held growth rate ("yield class") data for the crop planted in each sub-compartment. The average duration of each sequential growth stage was derived from a yield class/age model (Ratcliffe and Petty 1986). Crops were then classified into successional stages (chapter 2, section 2.4.3.3) by species and planting year. Where mixtures of coniferous and deciduous trees were planted, stages were defined by the age of the coniferous species.

Of 14 original classes, pure coniferous crops were merged with coniferous and deciduous mixtures to avoid classes that contained null or very small proportions of

Figure 5.1. *Kielder Forest (dark green), the study area (light green), Deadwater Burn watershed (light grey), and Kielder Burn watershed (dark grey).*

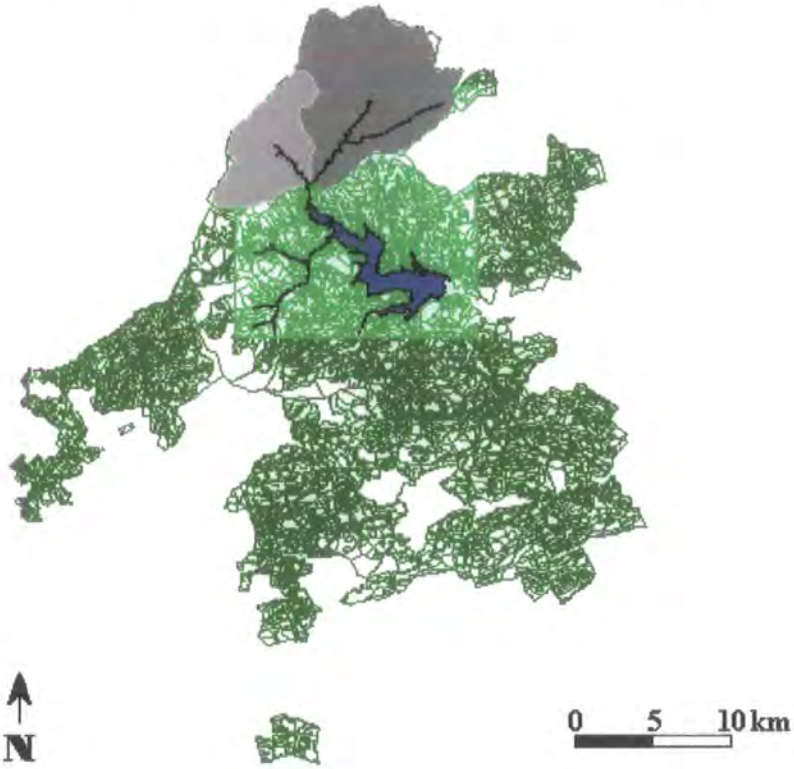
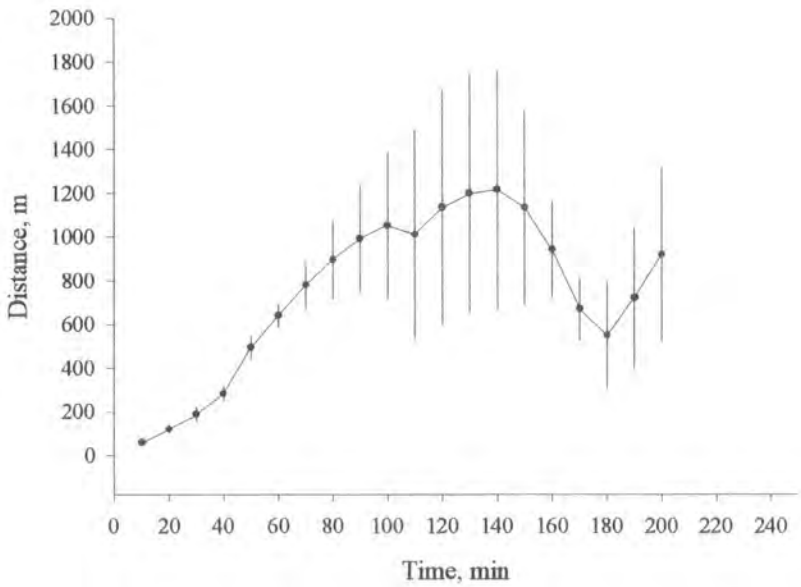


Figure 5.2. *Relationship between mean distance travelled and time since leaving the roost for three adult male tawny owls radio-tracked continuously for one full night. Error bars represent ± 1 SE.*



both availability and use. First-rotation pre-thicket and pure broadleaved crops were omitted because they formed less than 1% of the forest area and of areas used by owls.

Following Petty *et al.* (2000), 10% was added to the area of habitat suitable for field voles because forest stock maps did not include internal rides and other treeless habitats less than 10 metres wide. The final classes were as follows:

1) Thicket. Thicket stage crops of coniferous and mixed coniferous and deciduous trees.
2) Pre-felling. After the thicket stage, until the normal time of clear felling.
3) Extended rotation. Crops left to over-mature after the normal felling age.
4) Agricultural land. Mainly grazed sheepwalk and improved cattle pasture.
5) Habitat suitable for field voles. This class was composed of the following:
   i) Second rotation pre-thicket stage tree crops (suitable from one to x years after planting. X was the age at which the pre-thicket stage ended, derived from average yield classes. 15 years was used for broadleaved crops, although more ground vegetation persists throughout each stage than with spruce crops (S.J. Petty, personal communication).
   ii) Unplanted streamsides and deer glades
   iii) Miscellaneous unplanted land, for example, roadside verges.
0) Miscellaneous. Land uses not covered by other classes, such as recreation, and failed, felled or windblown tree crops. Originally, each sub-compartment was given a zero designation in the habitat class field, and hence this class represented those that remained unclassified after programs had been run to categorise classes 1) to 5).

5.2.3.2 Defining habitat availability

The habitat composition of the study area was compared to that of Kielder Forest. A compositional analysis was then performed to compare habitat composition of the entire area "familiar" to owls (= "use"), the minimum convex polygon (MCP) outline formed by joining the outer fixes for each bird (e.g. Kenward 1987), with that of the study area (= "availability"). In addition to this traditional definition of habitat availability, I then compared habitat composition of MCP outlines with that of the

watershed in which territories were located, as a second local and less arbitrary quantification of environmental composition.

Minimum convex polygon (MCP) outlines were used to quantify habitat use because polygons are particularly suited to coarse-grained habitats with abrupt boundaries, such as plantations, clear-cuts and other human creations (Kenward, in press). Their suitability would have been reduced if home ranges were adjacent to Kielder Water because they may then have encompassed part of the reservoir. This was not the case for the birds radio-tagged in this study. Although the area of MCP outlines is sensitive to fix sample size (e.g. Robertson *et al.* 1998), the absolute area was less important in this analysis than fitting home ranges to habitat boundaries.

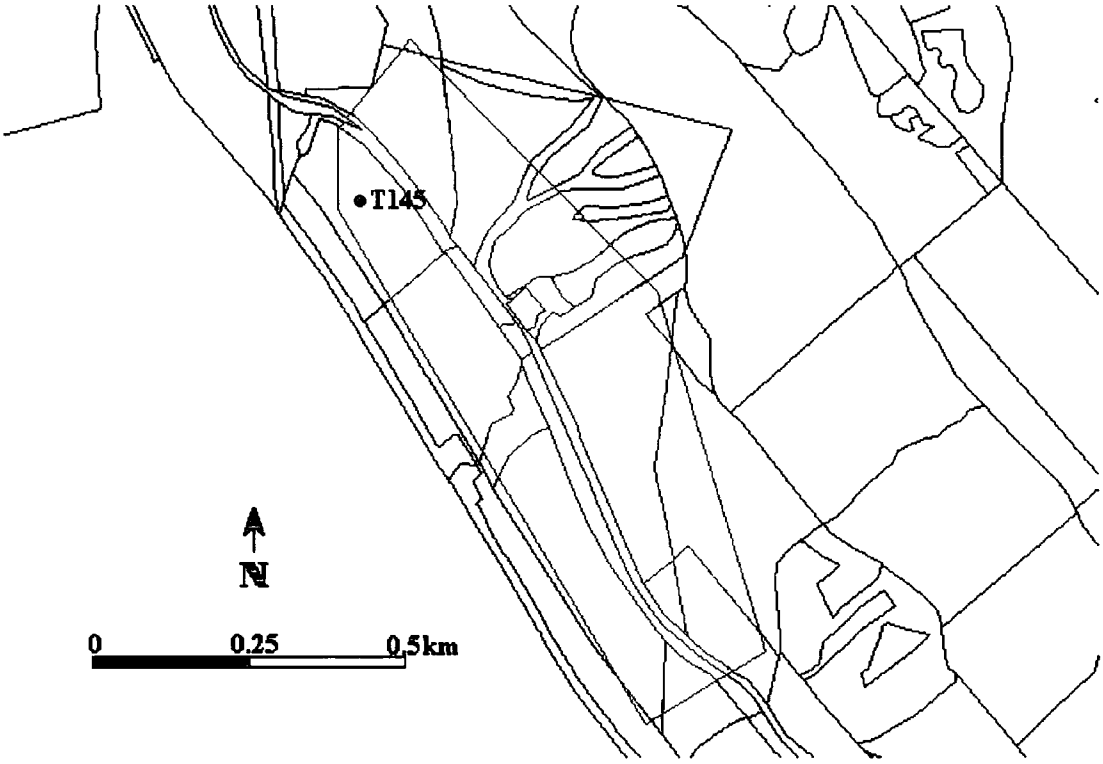
5.2.3.3 Data extraction

The reclassified forest database represented the composition of Kielder Forest as a whole. Proportions of habitat types present were calculated by summing the areas of occurrences of each type and then dividing by the total area of the forest. "Clipping" the re-classified Kielder Forest GIS coverage with overlay coverages created of the study area, watersheds and MCP polygons formed new "clip" coverages (figure 5.3). These extracted habitat composition data for the area of the forest that they covered, rather like shapes formed from a pastry cutter. Data were exported to database files, and proportions of each habitat type were calculated following the same procedure used for the whole forest.

5.2.3.4 Compositional analysis

This technique examines proportional habitat use by individual animals as a basis for analysis (Aebischer *et al.* 1993). Use of each habitat was expressed relative to each of the other habitats, as the log-ratio $\ln(U_i/U_j)$, with availability the equivalent $\ln(V_i/V_j)$. The difference in log ratios $\ln(U_i/U_j) - \ln(V_i/V_j)$ indicated preference between pairs of habitats and scored zero where animals had a similar association with each member of the pair. A chi-squared equivalent derived from Wilk's lambda was calculated to provide an overall statistic to test whether overall habitat use was non-random for the resulting matrix of pair by pair values. Both construction of matrices and calculations were performed by an MS-DOS program written by S. Rushton (University of Newcastle) using text files of percentage data. Null values in

Figure 5.3. *A GIS "clip" coverage (blue) of the MCP home range for adult male GF82758. This overlay on the reclassified Kielder Forest coverage (black), performed in ArcInfo, extracted data on the area and composition of each of the smaller polygons and thereby quantified habitat use of that individual. The nest box (T145) location is shown by a black dot.*



the MCP habitat use file were replaced by 0.001 - a figure of two magnitudes less than the smallest recorded percentage, to preserve the meaning that use of that habitat type was too small to be detected, as suggested by Aebischer *et al.* (1993).

Relative abundance of habitat types in MCP home outlines was compared to that in the study area, and in the Deadwater Burn watershed (section 5.2.3.2). The study area analysis included data for 14 birds of both sexes and from 1996-1998, but excluded data from the second year when the same birds were radio tagged in consecutive years. To rank the habitat types in order of use, a log-ratio difference matrix was set up in a spreadsheet and at each position in the matrix, the mean and standard error of the elements were calculated over all 14 birds. The ratio mean/standard error gave a t value at n-1 (where n = no. birds) degrees of freedom with which to test whether preferences differed significantly from zero for each habitat pair.

The second analysis was limited to birds with territories in the Deadwater Burn watershed because the number of birds radio tagged in the Kielder Burn watershed was insufficient to perform compositional analysis at that level. Similarly, differences between the habitat use of the two sexes, and between birds in the two valleys, were not investigated because a sample size of at least six individuals in each group is required (Aebischer *et al.* 1993).

5.2.4 Home range characteristics

5.2.4.1 Choosing a home range estimator

I collected 18-40 (mean 24.9) independent fixes per individual owl. Due to the sensitivity of MCP home range size estimates to fix sample size (section 5.2.3.2), corrections must be made if the numbers of fixes used are smaller than those required to reach size asymptotes in plots of range area against the number of fixes included (utilisation plots). An approximate minimal number is 25 fixes (Kenward, in press). For data collected in this study, the rate of size increase per fix added was non-linear and unpredictable (for example, figure 5.4). This meant that MCP area estimates could not be corrected (for method see Village 1982) for pre-asymptotic ranges.

In this part of the study, the size of ranges was more important than the precise positioning of outlines, for which the MCP technique was useful (section 5.2.3.2). Estimates calculated using the harmonic mean method are not as sensitive to fix sample sizes as those that use polygon estimators (Robertson *et al.* 1998, Kenward, in press). In addition, MCP estimates are highly influenced by peripheral fixes (Harris *et al.* 1990) and give no indication of how intensively an animal uses different parts of its range.

Harmonic mean home range estimates generally begin to stabilise at around 15 fixes (Kenward, in press), but produce less stable size asymptotes than the MCP technique (Harris *et al.* 1990). In practice, utilisation plots on 18 individuals revealed that home range areas became stable at around 16 to 32 (mean 21.4) fixes (figure 5.5a). A 40x40 grid was used.

The harmonic mean technique is based upon areal moments and allows for more than one centre of activity (Dixon and Chapman 1980). Although this technique produces configurations that relate well to the actual distribution of fixes, it is sensitive to highly skewed distributions (Harris *et al.* 1990). Therefore, it is desirable to visually compare fixes with the harmonic mean range estimate to check for misrepresentation.

Preliminary analyses showed that the positions of 100% harmonic mean contours were sometimes pulled toward outlying fixes, which represented unusual forays, and thereby grossly exaggerating the size of home ranges to include large areas that were not visited. Examination of utilisation (home range size versus the percentage of fixes included) plots provides a method of deciding on the percentage of fixes that define a core range. A perfect, objective core estimation technique has still to be developed, but this method can give a good indication (Kenward and Hodder 1996). If there are a few fixes far from the range centre, the slope of the plot is steep at higher percentage inclusion, but becomes shallower when only the core fixes remain. This was the case for many harmonic mean estimates of adult home ranges in this study (figure 5.5b). Figure 5.6 illustrates this point for an adult male radio tagged in 1997. One fix far to the west of the range centre distorts the 100% isoline (figure 5.6a), but this was identified in an individual utilisation plot (figure 5.6b) and the 95% core was used for

Figure 5.4. *Non-linear and unpredictable MCP home range area increase as fixes were added successively for adult male GF01186.*

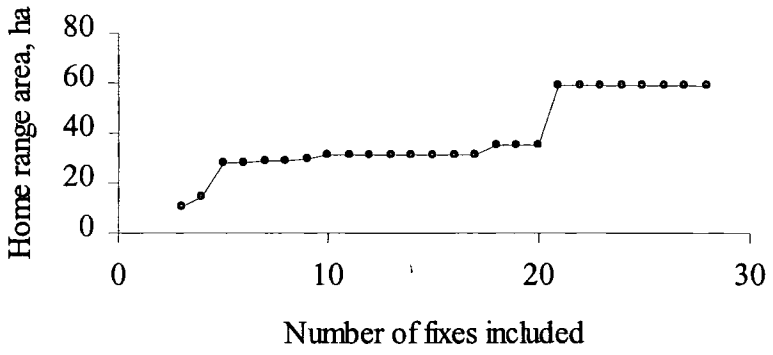


Figure 5.5 *Mean a) incremental area and b) utilisation plots for 100% harmonic mean home ranges of 18 adult tawny owls, radio tagged from 1996-98. Error bars show 95% confidence limits.*

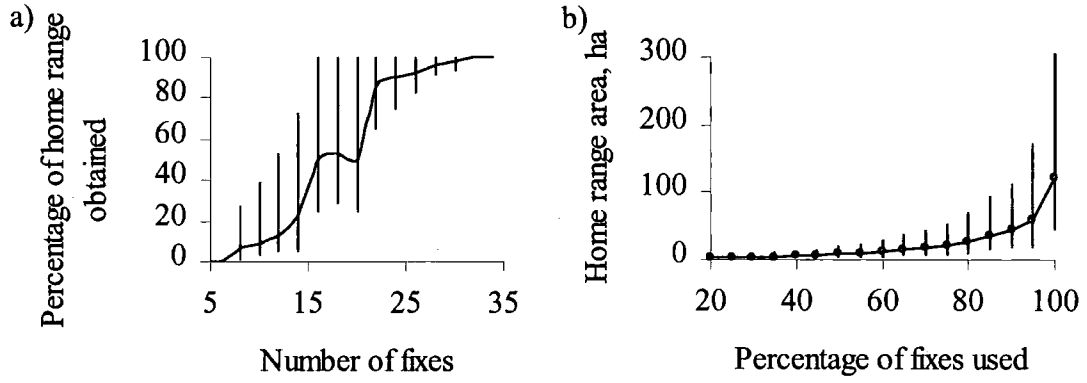
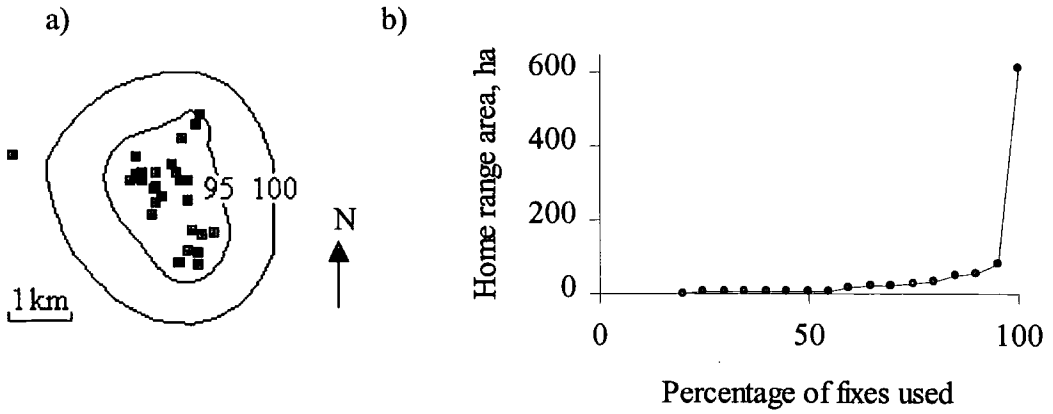


Figure 5.6 *a) 95% and 100% harmonic mean home range outlines and fixes, and b) utilisation plot for radio tagged adult male GF78041.*



an area estimate. Table 5.1 in section 5.3.1 gives the percentage inclusion core used for each of the birds radio tagged from 1996-98. Henceforth, these cores are referred to as "home ranges".

Home ranges of males radio tagged in 1998 were calculated using sub-sampled continuous data, collected exclusively during the breeding period. Therefore, home range area analyses were performed both with and without these individuals so that any effect upon the outcome could be assessed. Adult home range areas were positively skewed after log transformation and, therefore, non-parametric statistics were used throughout. Only data from the first year were included for birds radio tagged in consecutive years.

5.2.4.2 Home range overlap

The spatial overlap between home ranges was expressed as the percentage of each home range that was overlapped by another. Comparisons were made between ranges in Deadwater 1996, Kielder Burn in 1997, sexes, and between years for birds radio tagged in consecutive years. Comparisons between overlap of ranges in Deadwater 1997, and those of birds followed continuously in 1998, were omitted because there were several intervening territories between them where adults were not radio tagged (section 5.3.2).

5.2.4.3 Home range area and foraging habitat

Following Kenward (1982), I looked for correlations between both the proportion and absolute amount of grassy habitat suitable for field voles and individual variation in home range area. Log/log plots were used, which avoid the emphasis of small-range effects (Kenward, in press).

5.2.4.4 The length of habitat edges in home ranges

I produced clip coverages (section 5.2.3.3) of home ranges, extracted the data, and added together the length of each tree crop / grassland boundary in polygons to derive the total length of such edge habitat per home range. Edge length was then compared with home range size to investigate whether ranges increased in size until they contained a fixed length of edge, again in a similar fashion to Kenward's (1982) goshawk study.

5.2.4.5 Home range area in relation to prey density

In addition to the use of VSI sites within home ranges, I obtained an independent measure of the vole densities near each owl or pair of owls. In the absence of any data on territory size and structure in Kielder Forest, I used a circle with a radius of 589 metres, calculated from the mean home range area (109.1 ha) of all birds as a distance cut-off. These circles, hereafter referred to as "mean home range circles", were drawn around each nestbox and the mean vole density per territory was calculated as the average score of the VSI sites encompassed by each. The areas of home ranges were then compared with mean vole densities within them, and those in the respective mean circles. A separate comparison between home range size changes and changes in field vole abundance was made for birds that were radio tagged in consecutive years.

5.2.4.6 Nest box to clear-cut distance

The distance to the centre of the clear-cut nearest each nest box was measured, and the linear distances between nest boxes and the centre of all clear-cuts within the mean home range circle (section 5.2.4.4) were averaged for each territory. Clear-cuts used in this analysis were those that included a VSI site, and therefore satisfied the criteria of suitability for field voles. A clear-cut was included if its edge lay within the circle, even though its centre lay further away. This gave two measures of the distance of the available sources of field vole prey from each nest box, which were compared with variation in home range size. One territory had no patches within the mean home range circle. In this case, the distance to the nearest patch was used for both measures to reflect its highly dispersed food supply. Where more than one bird from the same nest box was radio tagged, mean home range sizes of all birds associated with that box were used because measures of food dispersion were the same for those individuals.

5.3 Results

5.3.1 Data collected

Eighteen adult tawny owls were radio tagged in the years 1996-98. Table 5.1 summarises the characteristics of each bird and the number of independent fixes collected for each. As a final check of the robustness of area estimates, I ensured that

there was no correlation between home range area and the number of fixes used to create them (Spearman's Rank correlation coefficient $r_s = 0.07$, $n = 18$, P = 0.79).

The habitat suitable for field voles in each of the valleys where birds were tagged was included in the seasonal VSI assessments detailed in chapter 3 (table 3.3). Thus, all clear-cuts and other suitable areas within home ranges of tagged adults were sampled. Additional vole abundance assessments were performed in 1998 and are detailed in chapter 6 (section 6.3.1).The numbers of sampling sites used in each analysis concerning vole abundance and variation between them are specified in the relevant sections.

5.3.2 Habitat use

5.3.2.1 Habitat characteristics of the forest and study area

Both the whole forest and the study area consisted mainly of (in rank order, largest proportion first), coniferous crops and coniferous/deciduous mixtures in the pre-felling stage, habitat suitable for field voles, and coniferous crops and coniferous/deciduous mixtures at the thicket stage (table 5.2). The proportion of agricultural land was slightly greater in the study area than in the forest as a whole, and crops at the felling and extended rotation stages comprised small proportions of both the forest and the study area. Overall, there was no significant difference between the proportions of habitat in the forest and those in the study area (Wilcoxon Signed Ranks test, Z = -0.11, $n = 6$, P = 0.92). Thus, the habitat composition of the study area was representative of that of the whole forest.

5.3.2.2 MCP outline and study area comparison

MCP estimates of the area with which each owl was familiar were 16.3-326.4 (mean 108.4, SE 20.8) hectares (table 5.3). Proportional composition of habitats enclosed by 14 MCP outlines, compared to habitats available in the study area, was significantly different from random (X^2 equivalent calculated from Wilk's Lambda = 13.27, df = 5, P = 0.021). A matrix of log-ratio differences was constructed and habitat types were then ranked according to utilisation (tables 5.4 and 5.5). The habitat types were ranked in the order: suitable for field voles > thicket > extended rotation > agricultural > miscellaneous > pre-felling. However, there was no detectable difference in the use of the top four habitats, implying that the order of

Table 5.1 *Basic information for 18 adult tawny owls radio tagged from 1996-98. "Valley" refers to Deadwater (DW) or Kielder Burn (KB). The number of independent radiolocations is given for each bird, alongside the percentage of harmonic mean isolines used to represent each home range. * = non-breeding bird.*

Ring no.	Freq.	Nest	Year	Sex	Valley	*n* fixes	Core %
GF73127	233	T145	1996	M	DW	26	95
GF01293	254	T6	1996	M	DW	18	95
GF01185	279	T3	1996	M	DW	21	95
GF01186	296	T120	1996	M	DW	22	95
GJ73143	909	T120	1996	F	DW	32	95
GH32604	919	T3	1996	F	DW	21	95
GH88229	960	T6	1996	F	DW	24	95
GH47748	973	T145	1996	F	DW	28	85
GF78041	531	T149	1997	M	KB	24	95
GF12929	553	T70	1997	M	KB	35	95
GF01185	562	T3	1997	M	DW	25	95
GF01186	573	T144	1997	M	DW	28	95
GF01169	804*	T1	1997	M	KB	18	100
GH32664	817	T3	1997	F	DW	40	95
GJ73143	829	T144	1997	F	DW	22	90
GF12931	422	T87	1998	M	DW	22	90
GF82759	441	T146	1998	M	DW	23	95
GF82758	500	T145	1998	M	DW	19	95

Table 5.2. *Percentage habitat composition within Kielder Forest, within the owl study area, in the Deadwater and Kielder Burn watersheds, and in 14 MCP home ranges. Habitat types one to three were successional forest stages. Vole refers to grassland suitable for field voles.*

Habitat type	Forest	Study area	Deadwater Burn	Kielder Burn	Home ranges (mean)
Thicket (1)	17.7	12.7	21.7	14.0	19.8
Pre-felling (2)	42.3	44.4	22.3	17.3	16.7
Ext. rotation (3)	1.1	2.1	2.5	0.8	13.2
Agricultural (4)	7.3	12.0	16.7	34.6	19.1
Vole (5)	21.9	21.0	29.0	30.6	26.8
Misc. (0)	9.9	7.9	7.8	2.7	4.6

Table 5.3. *MCP outline area estimates for 18 radio tagged tawny owls in 1996-98.*

Tag frequency	Year	Sex	Area, ha
233	1996	M	111.5
254	1996	M	42.0
279	1996	M	113.7
296	1996	M	167.0
909	1996	F	19.6
919	1996	F	50.7
960	1996	F	16.3
973	1996	F	61.7
531	1997	M	125.3
553	1997	M	263.3
562	1997	M	54.8
573	1997	M	59.9
804	1997	M	326.4
817	1997	F	68.8
829	1997	F	17.9
422	1998	M	217.5
441	1998	M	158.2
500	1998	M	76.7

Table 5.4. *Ranking matrix based on comparing proportional habitat use within MCP home ranges of 14 tawny owls with proportions of available habitat types in the study area. Mean log ratio differences and standard errors were obtained by averaging each element over all 14 birds.*

Habitat type	(1)	(2)	(3)	(4)	(5)	(0)
Thicket (1)		2.20 ±0.85	0.20 ±1.21	1.59 ±1.32	-0.02 ±0.27	1.82 ±0.87
Pre-felling (2)	-2.20 ±0.85		-2.00 ±1.63	-0.61 ±1.53	-2.21 ±0.92	-0.38 ±1.35
Extended rotation (3)	-0.20 ±1.21	2.00 ±1.63		1.39 ±1.81	-0.22 ±1.20	1.62 ±0.80
Agricultural (4)	-1.59 ±1.32	0.61 ±1.53	-1.39 ±1.81		-1.60 ±1.18	0.23 ±1.47
Vole (5)	0.02 ±0.27	2.21 ±0.92	0.22 ±1.20	1.60 ±1.18		1.83 ±0.80
Miscellaneous (0)	-1.82 ±0.87	0.38 ±1.35	-1.62 ±0.80	-0.23 ±1.47	-1.83 ±0.80	

Table 5.5. *Simplified ranking matrix based on comparing proportional habitat use within MCP home ranges of tawny owls with proportions of available habitat types in the study area. Each element in the matrix was replaced by its sign; a triple sign represents significant deviation from random at $P < 0.05$ ($t = mean / SE$, $df = 13$, $t_{crit} = 2.16$). Rows are ranked according to the number of positive values.*

Habitat type	(1)	(2)	(3)	(4)	(5)	(0)	Rank
Thicket (1)		+++	+	+	-	+	4
Pre-felling (2)	---		-	-	---	-	0
Ext. rotation (3)	-	+		+	-	+	3
Agric. (4)	-	+	-		-	+	2
Vole (5)	+	+++	+	+		+++	5
Misc.(0)	-	+	-	-	---		1

their assigned ranks meant little. Habitat suitable for field voles was used significantly more than miscellaneous land uses and pre-felling stage crops were used significantly less than both habitat suitable for field voles and thicket stage crops. There were no other detectable differences in utilisation.

5.3.2.3 Habitat characteristics of watersheds

Both watersheds contained higher proportions of habitat suitable for field voles and farmland, and less pre-felling stage crops than the whole forest and the study area did (table 5.2), although the habitat compositions of both watersheds were statistically similar to that of the study area (Wilcoxon Signed Ranks tests, Deadwater Burn: $Z = -0.73$, $n = 6$, $P = 0.46$, Kielder Burn: $Z = 0.11$, $n = 6$, $P = 0.92$). However, the habitat utilisation of 11 owls in the Deadwater Burn watershed did not differ significantly from random (X^2 equivalent, calculated from Wilk's lambda = 7.48, df = 5, $P = 0.19$).

5.3.3 Home range characteristics

5.3.3.1 General characteristics

Harmonic mean core home ranges tended to be large, covering 13.3-396.6 (mean 109.1, SE 25.5) hectares. Excluding birds radio tagged in 1997 that were also tagged in 1996, home range areas did not vary significantly between the three study years, and so data were pooled (Kruskal-Wallis ANOVA, $X^2 = 2.97$, df = 2, $P = 0.23$). It should be noted that because data were collected over several months, "overlaps" are inferred from core range outlines, rather than from direct evidence that owls shared the same space simultaneously.

5.3.3.2 Sex differences

Generally, male owls had larger home ranges than their mates did, but this difference was not statistically significant in either year (Wilcoxon Signed Ranks test, 1996: $Z = -1.83$, $n = 4$, $P = 0.068$; 1997: $Z = -0.45$, $n = 2$, $P = 0.66$) (tables 5.6 and 5.7). Female home ranges generally overlapped less than those of males, and in Deadwater Burn in 1996, male ranges included those of at least two females (tables 5.8 and 5.9, figure 5.7). Of those females, three out of four did not range outside the areas enclosed by the home ranges of their mates. The two largest and two smallest female ranges were grouped together at the northern and southern ends of the

Table 5.6. *Harmonic mean core home range areas and male/female overlap for four pairs of tawny owls radio tagged in the Deadwater Burn watershed in 1996.*

Nest box	Male	Female	% overlap M/F	% overlap F/M
T3	189.2	41.3	100.0	27.7
T6	17.8	15.3	100.0	32.1
T120	127.2	16.4	100.0	8.0
T145	134.7	90.0	100.0	61.3
Mean	117.2	40.7	100.0	32.3
SE	35.9	14.5	0.0	11.0

Table 5.7. *Harmonic mean core home range areas and male/female overlap for two pairs of tawny owls radio tagged in the Deadwater Burn watershed in 1997.*

Nest box	Male	Female	% overlap M/F	% overlap F/M
T3	38.5	73.6	42.0	68.9
T144	60.8	13.3	69.0	49.5
Mean	49.7	43.5	55.5	59.2
SE	11.2	30.1	13.5	9.7

Table 5.8. *Percentage overlap matrix for harmonic mean core home ranges of male tawny owls in the Deadwater Burn watershed in 1996. Range areas in rows are overlapped by range areas in columns.*

Bird radio frequency	233	254	279	296
233	-	1.8	49.9	42.1
254	5.6	-	0.0	77.1
279	41.3	0.0	-	2.1
296	34.0	19.7	2.0	-

Table 5.9. *Percentage overlap matrix for harmonic mean core home ranges of female tawny owls in the Deadwater Burn watershed in 1996. Range areas in rows are overlapped by range areas in columns.*

Bird radio frequency	909	919	960	973
909	-	0.0	0.2	10.1
919	0.0	-	0.0	32.6
960	0.2	0.0	-	0.0
973	0.0	17.8	0.0	-

Figure 5.7. *The harmonic mean core home ranges of four pairs of adult tawny owls in the Deadwater Burn watershed in 1996. Pairs are colour coded and males and females are shown by thick and thin outlines respectively.*

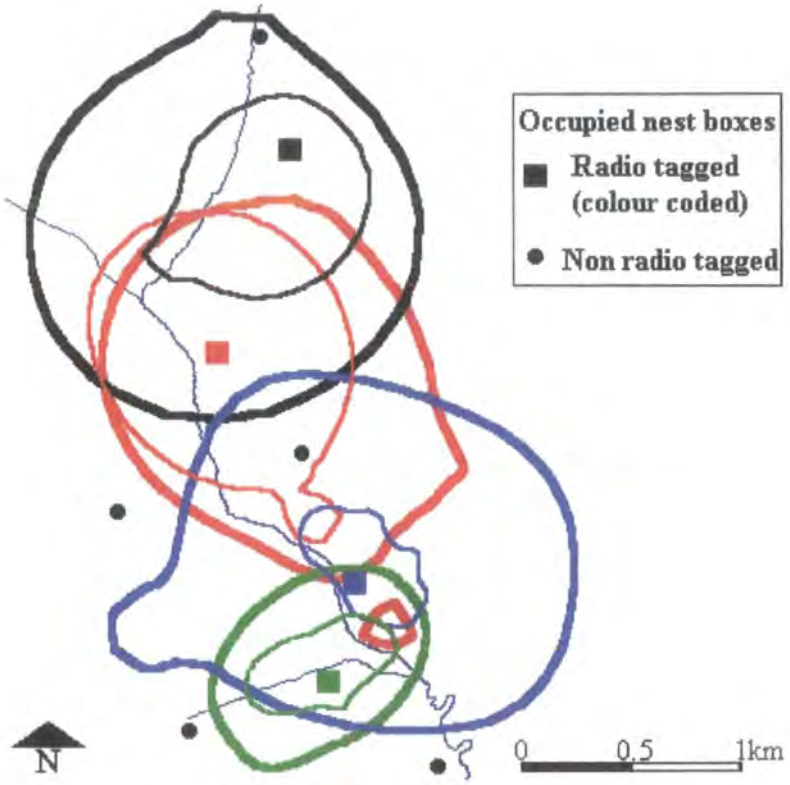
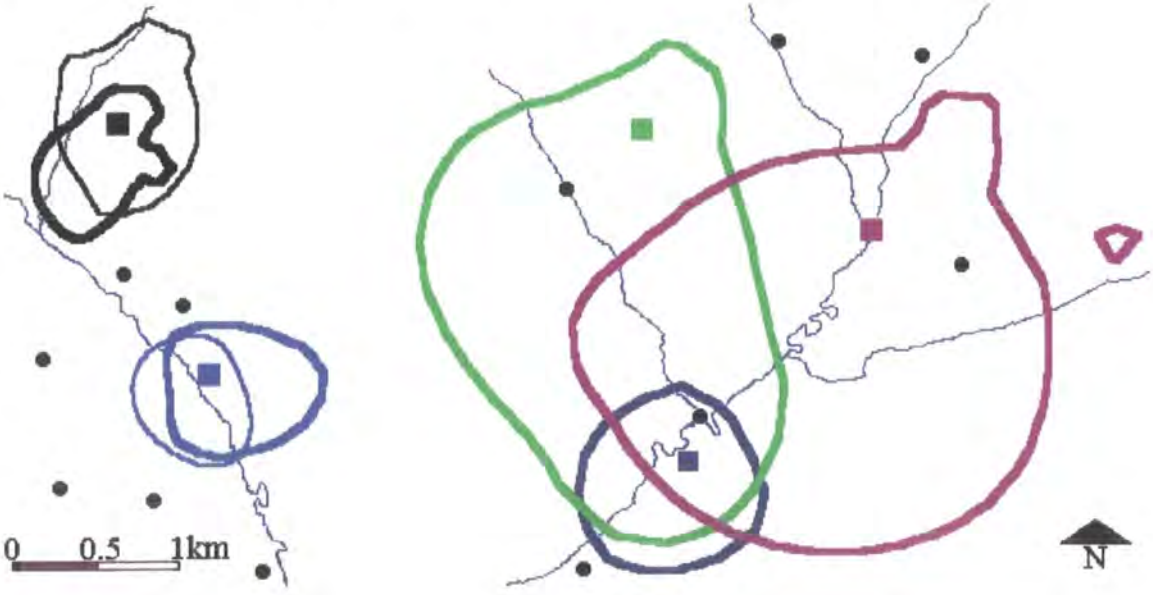


Figure 5.8. *The harmonic mean core home ranges of two pairs of adult tawny owls in the Deadwater Burn watershed and three adult males in the Kielder Burn watershed in 1997. Pairs or individuals are colour coded and males and females are shown by thick and thin outlines respectively. The same colours as in figure 5.7 were used for two Deadwater pairs radio tagged in consecutive years.*



Deadwater Burn, respectively. This was not the case in 1997, when male/female differences in range size and shape became less marked and overlaps between pairs, and between the two sexes, decreased (table 5.7, figure 5.8). The harmonic mean core home range area estimates using sub-sampled data from the three males followed continuously in 1998 are given in table 5.10.

5.3.3.3 Spatial differences

In 1997, birds were radio tagged simultaneously in two valleys. Home range sizes of all birds were significantly larger in Kielder Burn (table 5.10) than those in Deadwater Burn (table 5.6, figure 5.8) (Mann-Whitney test, U = 0.00, n = 4,3, P = 0.03). Sample sizes were too small for a males only statistical comparison, but both Deadwater males had smaller ranges than any of their Kielder Burn counterparts. Mean linear nest box to clear-cut distances were 132 and 752 metres in Deadwater Burn and Kielder Burn respectively. The relationship between home range area and food dispersion is discussed more fully in section 5.3.4.2.

Like those in Deadwater Burn, home ranges in Kielder Burn showed a high degree of overlap (table 5.11, figure 5.8), and on one occasion, all three radio tagged males from the Kielder Burn were located foraging at the edge of the same clear-cut, illustrated by the area of overlap that was common to all three home ranges. In 1996, there were three areas in the Deadwater Burn watershed where the home ranges of three males overlapped (figure 5.7). It is clear from the positions of occupied nest boxes where birds were not radio tagged that the actual degree of home range overlap in both of my study areas may have been even greater (figures 5.7 and 5.8), although direct evidence of simultaneous patch use was restricted to anecdotes such as that above.

5.3.4 Home range area in relation to habitat characteristics

5.3.4.1 Foraging habitat

Foraging habitat, that is habitat suitable for field voles, comprised 3.6-71.2 (mean 25.7, SE 3.4) % of all harmonic mean core home ranges (n = 18), the equivalent of 1.4-89.7 (mean 22.6, SE 5.6) hectares. The mean value was similar to that for the MCP outlines used in the compositional analysis (section 5.3.1.1, table 5.3).

Table 5.10. *Harmonic mean core home range sizes of adult male tawny owls in the Kielder Burn watershed in 1997, and of birds followed continuously in 1998. Continuous data were sub-sampled to derive fixes for home ranges.*

Group	Nest box	Range size, ha
Kielder Burn	T1	329.5
1997	T70	396.6
	T149	81.1
	Mean	269.1
	SE	96.0
1998 males	T87	185.1
	T145	120.1
	T146	33.1
	Mean	112.8
	SE	44.0

Table 5.11. *Percentage overlap matrix for harmonic mean core home ranges of male tawny owls in the Kielder Burn watershed in 1997. Range areas in rows are overlapped by range areas in columns.*

Bird radio frequency	531	553	804
531	-	78.8	51.0
553	16.3	-	37.3
804	8.6	30.3	-

Table 5.12. *Changes in harmonic mean core home range areas, overlap and mean vole density within home ranges for two territories where adult tawny owls were radio tagged in consecutive years.*

Nest box	Sex	Change in range area	% overlap 1996/1997	% overlap 1997/1996	Change in vole density
T3	Male	-150.7	100.0	19.6	+79
	Female	+37.3	76.6	88.9	+ 105
T120/T144	Male	-66.4	100.0	22.5	+36
	Female	-3.0	100.0	45.2	+35

There was no significant correlation between 14 home range sizes and the proportion of vole habitat within them (figure 5.9a). This was the case whether or not the 1998 males were included (Spearman's Rank correlation coefficients, with 1998 males: $r_s = 0.13$, $n = 14$, P = 0.67; without 1998 males: $r_s = 0.15$, $n = 11$, P = 0.67).

Since the proportion of vole habitat is part of the home range, there is a degree of dependence in plots of one against the other. However, the high degree of scatter suggested that this effect was negligible. Put another way, increasing home range areas encompassed increasing areas of vole habitat (figure 5.9b). This result was consistent with the results from the compositional analysis at the watershed level (section 5.3.1.3).

5.3.4.2 Forest/grassland edge

The total length of boundaries between tree crops and grassland varied from 0.47-6.10 (mean 2.56, SE 0.50) kilometres per home range. The length of habitat edges in individual home ranges was significantly correlated with home range area, and the degree of this correlation was similar whether or not the 1998 males were included (Spearman's Rank correlation coefficients, with 1998 males: $r_s = 0.72$, $n = 14$, P < 0.01; without 1998 males: $r_s = 0.73$, $n = 11$, P = 0.01)(figure 5.10). In other words, the length of grassland/woodland edge in home ranges increased as the amount of all habitats included increased.

5.3.5 Home range area in relation to prey abundance and dispersion

5.3.5.1 Field vole density

Comparing the home ranges of two pairs tagged in both years, all but one bird reduced its range size in 1997 (table 5.12, figures 5.7 and 5.8). However, these differences were not statistically significant (Wilcoxon Signed Ranks test, Z = -1.2, n = 4, P = 0.49). Mean vole density estimates in home ranges increased for each bird in the second year, but individual changes in range area were uncorrelated with the magnitude of change in vole densities (Spearman's Rank correlation coefficient, r_s < 0.00, $n = 4$, P = 1.00)(table 5.12).

Furthermore, home range areas in general were unrelated to mean field vole density estimates within them (Spearman's Rank correlation coefficient, $r_s = 0.15$,

Figure 5.9. *Log/log plots of harmonic mean core home range area against a) the proportion, and b) the area of foraging habitat in home ranges of 14 tawny owls radio tagged in 1996-98.*

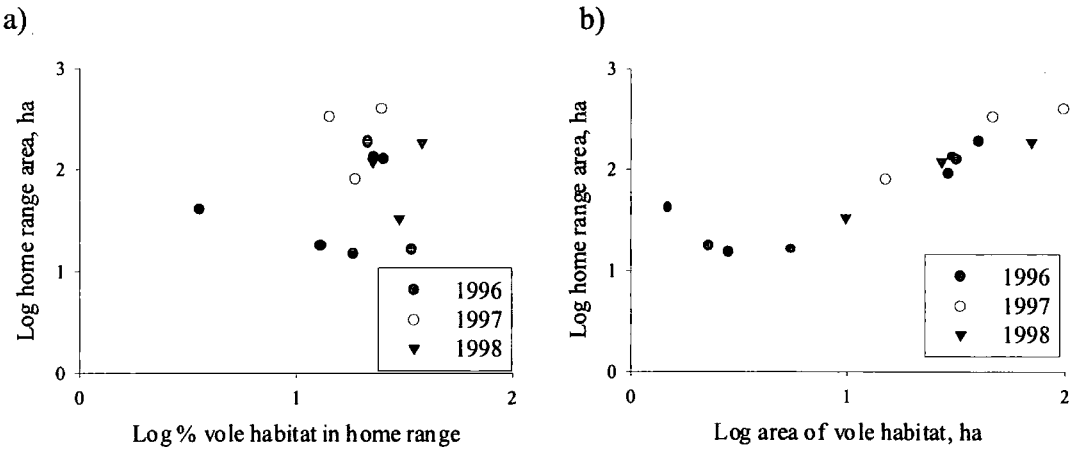


Figure 5.10. *Log/log plot of harmonic mean core home range area against length of grassland / tree edge habitat in home ranges of 14 tawny owls radio tagged in 1996-98.*

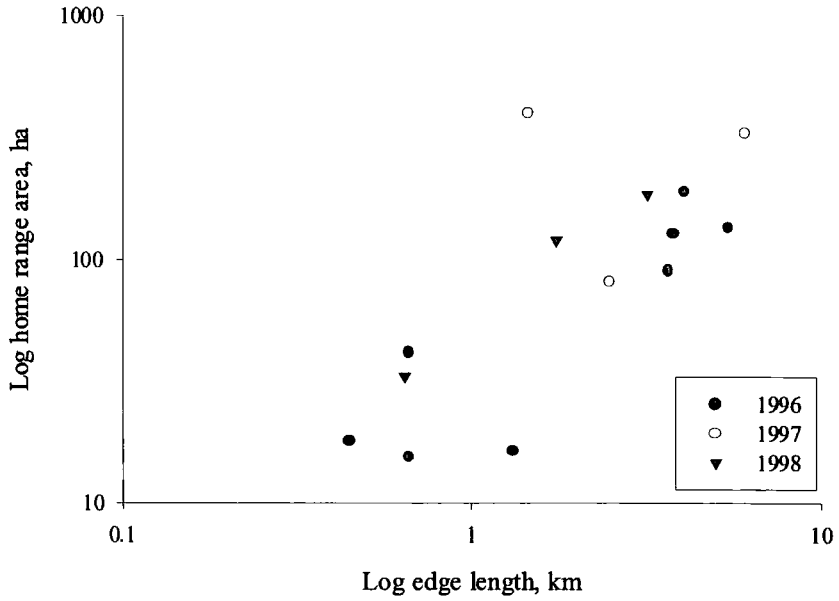
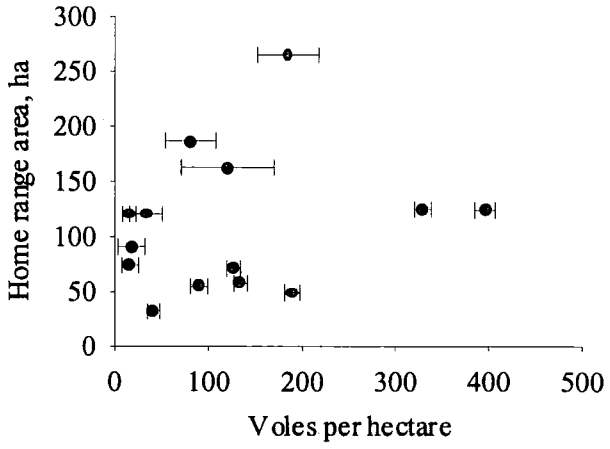


Table 5.13. *Voles per hectare in harmonic mean core home ranges of 14 tawny owls radio tagged from 1996-98. Numbers of assessment sites, minimum and maximum densities at those sites, and CVs are also given for each range.*

Bird radio frequency	Year	*n* sites	Min	Max	Mean	CV (%)
233	1996	19	15	127	58	53
254	1996	5	57	127	91	36
279	1996	13	15	127	49	59
296	1996	18	15	127	71	44
909	1996	9	43	127	74	35
919	1996	4	15	43	32	42
960	1996	2	113	127	120	8
973	1996	14	15	127	55	64
531	1997	7	37	252	187	38
553	1997	29	37	252	124	47
804	1997	39	37	252	125	45
422	1998	4	184	325	265	25
441	1998	6	43	297	163	75
500	1998	10	29	226	120	46

Figure 5.11. *Mean vole density estimates (± 1 SE) within harmonic mean core home ranges of 14 adult tawny owls (x), radio tagged in 1996-98, and range area (y)*



n =14, P = 0.61)(figure 5.11). Home ranges encompassed several clear-cuts that included a number of VSI assessment sites, and the vole density estimates at these sites were highly variable (table 5.13). In addition, the mean vole densities inside mean home range circles were also uncorrelated with home range areas (Spearman's Rank correlation coefficient, $r_s < 0.00$, $n = 14$, P = 1.00). Vole density estimates within circles ranged from 57-271 (mean 183, SE 18) animals per hectare. Neither of these analyses produced statistically significant results when males radio tagged in 1998 were removed. This was also the case when data for the two sexes were analysed separately.

Multiplication of mean vole density per home range by the area of vole habitat within the range gave absolute abundance estimates of 48-18620 (mean 3842, SE 1422) voles per range. These estimates were strongly correlated with home range area (Spearman's Rank correlation coefficient, $r_s = 0.81$, $n = 14$, $P < 0.01$).

5.3.5.2 Food dispersion.

Mean home range circles encompassed 0-4 (mean 2.5) potential foraging areas (table 5.14). Although there were insufficient data to investigate seasonal changes in space use, individual birds foraged in the same areas throughout the tracking periods. The centres of clear-cuts nearest to nest boxes were 0.14-0.95 (mean 0.36, CV 62%) kilometres away. Mean linear distances from nest boxes to all clear-cuts within mean home range circles ranged from 0.30-0.95 (mean 0.51, CV 31%) kilometres. Thus, the average distance to all food sources available within mean home range circles was less variable than the distance to the closest food source.

The distance to the nearest clear-cut was significantly correlated with home range area (figure 5.12), but this was not the case for the mean distance to all clear-cuts available to birds in each territory (figure 5.13). One analysis included data from both sexes, using mean home range area values where more than one bird had been radio tagged from each territory (Spearman's Rank correlation coefficients, nearest patches: $r_s = 0.82$, $n = 10$, $P < 0.01$; all patches: $r_s = 0.56$, $n = 10$, P = 0.10). These results were similar when males radio tagged in 1998 were removed ($n = 8$, P = 0.01 and 0.05 respectively).

Table 5.14. *The distances to centres of nearest clear-cut patches, and mean distances to all clear-cut patches within mean home range circles of 10 tawny owl territories where at least one bird was radio tagged in 1996-98. Also given are the numbers of home ranges, and their areas, used in each comparison with food dispersion. Mean values were used where more than one bird was radio tagged in any one territory.*

Territory	Nearest clear-cut, km	Mean distance to all clear-cuts, km			Mean range area per territory, ha (all)			Mean range area per territory, ha (males)		
		n	Mean	SE	*n*	Mean	SE	*n*	Mean	SE
T1	0.45	2	0.57	0.12	1	329.5	-	1	329.5	-
T3	0.25	2	0.48	0.23	4	85.7	35.4	2	113.9	75.4
T6	0.14	3	0.47	0.17	2	16.5	1.2	1	17.8	-
T70	0.39	3	0.59	0.11	1	396.6	-	1	396.6	-
T87	0.95	1	0.95	-	1	185.1	-	1	185.1	-
T120	0.37	4	0.48	0.06	2	54.4	26.6	1	127.6	-
T144	0.22	4	0.52	0.11	2	37.1	23.7	1	60.8	-
T145	0.31	2	0.50	0.19	3	86.0	29.4	2	83.9	50.8
T146	0.30	1	0.30	-	1	120.1	-	1	120.0	-
T149	0.24	3	0.52	0.16	1	81.1	-	1	81.1	-

Figure 5.12 *The relationship between the distance to the nearest clear-cut patch from 10 tawny owl nest boxes and home range area (± 1 SE for mean values) of the adult owls (total* n = *18) associated with each nest box in 1996-98.*

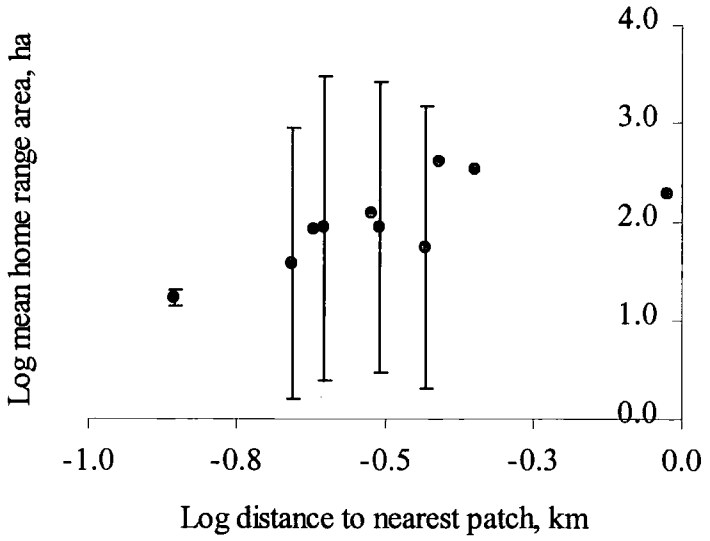
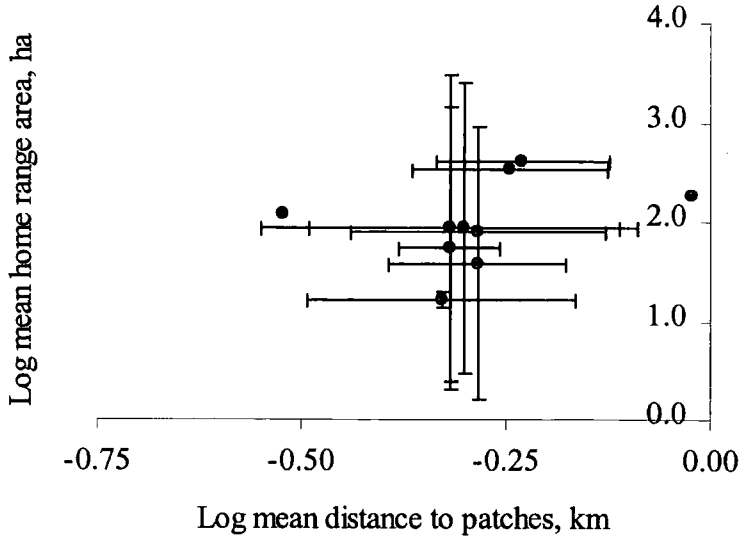


Figure 5.13 *The relationship between the mean distance to all clear-cut patches (± 1 SE) within a circle with an area of the mean tawny owl home range in Kielder Forest from 10 nest boxes, and home range area (± 1 SE for mean values) of the adult tawny owls (total* n = *18) associated with each nest box in 1996-98.*



Including males only, again with mean values for territories where more than one bird had been radio tagged over the three years of the study, the results were similar (Spearman's Rank correlation coefficients, nearest patches: $r_s = 0.86$, $n = 10$, P = 0.002; all patches: $r_s = 0.48$, $n = 10$, P = 0.16). Once more, removal of males radio tagged in 1998 did not alter the results significantly ($n = 8$, $P < 0.01$ and 0.10 respectively)

5.4 Discussion

5.4.1 Data considerations

5.4.1.1 Choice of home range estimators

Different estimators were used for different sets of analyses, because no one technique is appropriate for every question, or every data set (Kenward, in press). The compositional analysis was based upon the entire "familiar" area (MCP outline) and was directly comparable with similar studies. Home range analyses related to my best estimate of the area used regularly, with the fix sample sizes available.

Future data collection regimes would be organised so that sample sizes were sufficient to calculate home ranges on a seasonal basis, and to ensure that each range had reached its asymptotic size when estimated using analysis techniques chosen *a priori*. Ideally, enough fixes would have been collected to have identified polygon cores, rather than harmonic mean isopleths. This is because polygonal representations are well suited to Kielder's geometrical landscape structure. To increase the rather low power of some statistical tests in this study, a greater number of individuals should be tagged, perhaps concentrating entirely upon one sex to reduce the number of variables.

5.4.1.2 Time to statistical independence of continuous follow data

The time after which the distance an owl had travelled from its roosting site no longer increased was similar in Kielder Forest to the 120 minutes found for tawny owls in fragmented lowland woodland (Redpath 1995). This limited evidence may suggest that movement rate was similar in a relatively continuous habitat to that in a more fragmented one.

Temporal autocorrelation was a major limitation in the amount of useful home range data that could be collected. Rooney *et al.* (1998) suggested that, due to the compromise of data quality inherent in sub-sampling, the best possible estimation of home range size would be the repeated use of as short a sample interval as is possible over an extended period of time. In this study, an average of around two independent fixes was collected in any one night. Although this regime yielded high quality data, sample sizes were compromised. The range area estimates of three males followed continuously in 1998 may have been reduced by the effects of sub-sampling, as reported by Rooney *et al.* (1998). In addition, none of the data used in their calculation were collected outside the breeding period and this in itself may have influenced their area. Therefore, analyses were performed both with and without the data from these birds where possible.

5.4.1.3 Effects of radiolocation error on detecting habitat use

Intuitively, the power of statistical tests to detect habitat selection decreases as the proportion of erroneous radiolocations increases (White and Garrott 1986). However, using the home range as the definition of habitat use largely eliminated the potential effects of assigning individual fixes to the wrong habitat class. Although the area of home ranges may be influenced to an extent by radiolocation error (Springer 1979), small changes in the positions of home range boundaries were unlikely to have greatly affected the proportions of habitats within them.

5.4.2 Habitat selection

I would also apply the above argument to the use of data for 1998 males in the compositional analyses. It was clear from my data that home ranges of different areas were roughly similar in habitat structure and composition. The home ranges of males radio tagged in 1998 encompassed all the main activity areas of these birds, and proportional habitat composition was unlikely to have differed considerably with a small size change in size which may have occurred outside the breeding period, or by using unsampled, independent data. Field vole populations were largely confined to clear-cuts (Thomson 1996) and owls had relatively little choice as to where they hunted for them. Therefore, I suggest that adults were unlikely to have used an entirely new set of hunting areas at the onset of independence of their offspring.

Had I regarded an arbitrarily defined study area as the definitive representation of habitat availability to owls, I would have launched into a series of explanations as to why certain habitat types appeared in MCP ranges in preferential proportions to others, and the implications for forest management. However, I showed that after subdividing the study area in a non-arbitrary manner, the apparent selection of grassland and thicket-stage crops above their (spatial) abundance in the landscape "disappeared", and birds simply included habitats in their home ranges in roughly the proportions available to them in the "local" environment. This was reinforced by the strong correlation between home range areas and the absolute amount of vole habitat within them. Although the difference between habitat composition of the study area and watershed was not statistically significant, it was sufficient to have affected the outcome of the compositional analyses.

Higher breeding densities were supported where the habitat mosaic was finer-grained, yielding more edge habitats (Petty 1989) and numbers of tawny owls increased as clear-cutting provided profitable foraging areas (Petty 1989, 1992). Although the number of territories per unit area declined with increasing altitude (Petty 1992), the tawny owl study area was populated throughout. Thus, birds have "chosen" to inhabit areas other than the watersheds where my radio tagged sample held territories, with their particular habitat characteristics that differed subtly from other areas of the forest. I suggest that settling patterns are probably more closely related to territorial vacancies where nest boxes are provided than to "selection" for certain habitat characteristics in different parts of the study area. It may be that Kielder Forest itself is an appropriate scale at which to further examine the habitat selection of this entire tawny owl population, using home ranges or radiolocations of a large number of birds distributed randomly. The question of spatial scale is discussed further in chapter 7.

Although the home range reduces dependence upon accuracy of individual fixes (section 5.5.1.3), it also includes potentially large areas that were traversed but otherwise unused (e.g. Kenward 1987). Therefore, the results of my analyses were only useful in determining how the contents of home ranges of my sample group related to the habitat types available. Further analyses at a variety of scales *sensu* Johnson (1980) could be performed to answer different questions (Aebischer *et al.*

1993). For example, whether habitat use at radiolocations ("actual use") differed from that available at home range level, and whether core ranges (the "usual" area) differed in composition from the home range as a whole - the "familiar area" (e.g. Hodder *et al.* 1998).

5.4.3 Home range characteristics

The trend for larger home ranges in males than females was consistent with previous findings (Appleby 1995, Redpath 1995). Tawny owls are short-winged and dumpy (Petty 1992), with higher wing loading in the heavier females making sustained flight more costly (Appleby 1995). Another explanation is that females were more tied to fledged broods. Prior to fledging, the female defends the brood (S.J. Petty, unpublished data). Whether or not the difference between the areas of male and female home ranges persisted after the breeding period could not be tested using my data, but anecdotal evidence suggested that birds continued to forage in similar areas after young became independent.

As with this study, Appleby (1995) reported little overlap between female ranges, but large overlap of male ranges with those of females and other males. Bigamy has been reported before for the tawny owl (Hirons 1976, Appleby 1995), but not in Kielder Forest, although my results suggest that the potential did exist, with various caveats for the conclusions drawn from overlap results as set out below. No data on territorial behaviour were collected, so I could not confirm whether the area defended by each sex were similar, as in Wytham Woods (Appleby 1995).

5.4.4 Home range area in relation to foraging habitat and food supply

Unlike some other studies, which showed that home range or territory size varied in relation to primary prey density (e.g. Myers *et al.* 1979, Village 1982, 1987, Zabel *et al.* 1995), my results indicated that home range sizes were not related to prey abundance. Strong positive correlation between the estimated absolute number of voles and home range size is the opposite to what is expected if animals increase their range area to include sufficient food resources. However, this estimate assumed equal abundance across all habitat "suitable" for colonisation by field voles and may have reflected the difficulty in producing separate estimates for patches smaller than the 0.25ha required for VSI assessment.

Within any of the home range estimates, vole abundance was highly variable. Some of the density estimates for home ranges were based upon small numbers of assessment sites and were more prone to error than the majority, which were based upon a larger number (Lambin *et al.* 2000). They represented a best estimate of relative vole densities where time constraints did not permit live trapping. Chapter 7 discusses sampling errors inherent in the VSI technique.

Home range outlines were used when deciding which VSI sites should be included for estimates of prey abundance within them. VSIs within circles of the mean home range diameter for owls in this area of the forest were used as a supplementary check against criticisms of lack of independence, but were less meaningful when judging exactly where owls may have obtained food. In the absence of any home range or foraging information whatsoever to justify inclusion of multiple patches, different criteria were adopted for VSI sampling site choices for the broods or individuals studied in chapters 3 and 4.

Another issue that applies throughout this thesis is the discrepancy between numbers of voles present, and what is available to foraging owls. The limitations that this incongruity imposes upon the VSI technique are explored in detail in chapter 3. My analysis using edge length partly dealt with variation in prey availability to a perch-hunter caused by differences in habitat structure. The shape of plantations affects their edge length and, assuming that hunting occurs from edges, the profitable foraging area. Further refinements may include estimation of the distance over which an owl can hunt profitably from its perch so that estimates of foraging habitat are reduced accordingly. However, the resolution of radio tracking data (chapter 2) and difficulty of making direct observations in this environment (chapter 6) may pose problems for such an approach. The foraging behaviour of tawny owls in relation to variability in field vole density is discussed in chapter 6.

To some extent, the areas used by tawny owls in Kielder Forest reflected the dispersion of their main food supply. The importance of clear-cuts was underlined by the areas where the home ranges of three owls overlapped in both valleys. However, were these interactions dynamic, rather than being simply an artefact of unusual excursions, and the fact that data were collected over several months? Anecdotal

observations of up to three radio tagged birds located simultaneously around the same clear-cut certainly showed that patches were shared at least occasionally. Secondly, the most unusual excursions were excluded by the use of core ranges. Given the locations of untagged pairs, the actual degree of overlap may have been much greater than was revealed by radio tagged pairs. If these patterns are real, they are more consistent with colonial or semi-colonial species than highly territorial species, such as tawny owl (Newton 1979). The patchy and rather centralised nature of the food supply in Kielder Forest, where very low densities of rodents are present beneath the canopy (J.L MacKinnon unpublished data, Petty 1992, Thomson 1996, Lambin *et al.* 2000), may explain any tendency toward resource sharing. However, due to the limited evidence of overlap in space use on the same day, further work would be required to understand the true nature and extent of dynamic interactions. Simultaneous continuous follow tracking by multiple observers of owls from adjacent territories and over an extended period may provide the necessary data.

Food dispersion could not have accounted for the patterns exhibited by the range areas of the pairs radio tagged in consecutive years, when the distance to surrounding clear-cuts remained similar. The three home range contractions may be explained by a temporal change in prey abundance, but the increase in the home range of one female was anomalous with either the food dispersion or abundance explanations. It was possibly related to a vacancy that appeared in an adjacent territory, given that female ranges seemingly overlapped less than those of males did, and that territory size in tawny owls is strongly influenced by breeding density (Hirons 1985b).

The results of this study did not meet another of the RDH's predictions - that home ranges would encompass similar areas of fruitful habitats. There were close positive correlations between both the area of vole habitat and the length of habitat edge within home ranges and home range size, reflecting the homogeneous nature of this habitat. Inclusion of more habitat in larger home ranges simply included grassland and habitat edge in similar proportions to their availability. However, my results were not necessarily inconsistent with the hypothesis that the animals were encompassing an area large enough to meet their feeding needs (e.g. Kenward 1982) if owls were defending an area large enough to support them in a poor food year, thus allowing for variability in vole abundance.

Alternatively, it is possible that harmonic mean core ranges excluded some unfruitful habitat and therefore biased the results. All the main range area analyses were repeated with MCP estimates and derived data, with no change in the results. Only the results obtained using the harmonic mean technique were presented here for reasons of brevity and clarity. Moreover, I set out to investigate if the area *normally* used conformed to the RDH, rather than that included by rare excursions.

Redpath (1995) illustrated the importance of habitat fragmentation to a tawny owl population. The prediction that the degree of fragmentation of fruitful habitats should affect range dispersion was one of those arising from the RDH that this study did not consider in detail. As well as the distance to the nearest food source, factors such as patch size, shape and juxtaposition may be important. Further work, using an advanced spatial statistics package such as FRAGSTATS, could quantify any such relationships.

5.5 Summary

The aim of this chapter was to compare home range composition of territorial tawny owls to habitat composition of i) the study area - an arbitrary boundary, and ii) the watershed, a sub-division with biological relevance, and to examine characteristics of home ranges in relation to the abundance and dispersion of field voles. Home range data were collected for 18 birds over three years.

Kielder Forest, the tawny owl study area and the watersheds of Deadwater Burn and Kielder Burn all consisted of mainly pre-felling stage plantation crops, grassland suitable for field voles, and thicket stage plantation crops. Fourteen tawny owl foraging ranges used in analyses did not encompass random proportions of habitat types with respect to the composition of the study area - habitat suitable for field voles, was significantly more abundant than pre-felling stage plantations and miscellaneous land uses, and thicket stage crops were significantly more abundant than pre-felling stage crops. There were no other detectable differences between the spatial abundance of habitat types in the landscape and their inclusion in home ranges. However, composition of home ranges did not differ significantly from availability at the watershed level, confirming that the conclusions reached by such a study can depend upon the spatial scale of investigation.

Home range areas averaged around one square kilometre (harmonic mean core: 13.33-396.59 ha, mean 109.09 ha; MCP: 16.34-326.41 ha, mean 108.41 ha), seemingly with a high degree of overlap, particularly between males. However, data were collected over several months, and direct evidence of resource sharing was limited. Simultaneous tracking of two or more owls would be necessary to assess the degree to which space is shared on the same day.

Male birds of radio tagged pairs generally had larger home ranges than their mates, but these differences were not statistically significant and became smaller between years as vole densities increased. In Deadwater in 1996, male home ranges included those of at least two females. The home ranges of birds in Kielder Burn were significantly larger than those in Deadwater Burn. This difference was associated with larger average distances between nestboxes and feeding areas. In both valleys, there was at least one area in which the home ranges of three radio tagged males seemingly overlapped.

The results of this study were partly consistent with the resource dispersion hypothesis, which states that territory (or home range) sizes of animals are determined by food dispersion. Home range sizes were not related to variation in field vole abundance between home ranges, but were significantly correlated with the dispersion of feeding areas around territories - more specifically, with the distance to the nearest clear-cut patch. However, the area of foraging habitat differed widely between home ranges, so that the proportion remained similar in each. The length of habitat edge – assumed to be a foraging resource for the perch-hunting tawny owl - similarly increased with increasing home range area. In both instances, tawny owls did not increase the areas they used to include a fixed amount of fruitful habitat. Suggestions are made for further work to investigate the role of additional factors in the range dispersion of tawny owls in this environment.

Chapter 6 Aspects of foraging behaviour of tawny owls in relation to spatial variation in field vole density

6.1 Introduction

Generalist predators may have a stabilising influence upon fluctuations of rodent populations, since they respond functionally to rodent abundance, and switch to alternative prey when rodents are scarce (Erlinge *et al.* 1983). Therefore, to quantify such influences, it is necessary to assess the response of these predators to variations in prey density.

Animals in a heterogeneous environment make choices over where to go, and how long to stay there (Charnov 1976). They make foraging decisions based on the current distribution of resources, previous experience, and their condition (Stephens and Krebs 1986). A predators' response to higher prey densities may depend upon its life history, the time-scale of the difference in densities, and the cost of increased foraging effort (Abrams 1991). Thus, the responses of grand skinks *Oligosoma grande* to experimentally increased blowfly (Diptera: Calliphoridae) densities included changes in movement patterns and an increase in the space used (Eifler and Eifler 1999). Conversely, food-supplemented burrowing spiders *Seothyra henscheli* reduced their foraging activity, with the inference that foraging activity was risky and should be minimised (Lubin and Henschel 1996). Viswanathan *et al.* (1999) suggested that the success of random searches could be optimised by varying flight lengths so that long flights became increasingly rare as food densities at "target sites" increased, thus restricting the area covered during foraging. For great horned owls, the territorial system was largely resistant to extreme variations in prey density, but there was evidence that spatial use within territories centred on experimental "hot spots" of snowshoe hare abundance (Rohner and Krebs 1998). Owls have few, if any, nocturnal predators and therefore, may be more likely to increase their foraging effort in response to high prey densities than species for which foraging is more risky.

The proportion of a tawny owl population that breeds is strongly related to the state of small mammal populations. Those birds which do breed in periods with few rodents produce small clutches and broods, and use alternative foods (Petty 1999). However, when rodents are abundant, most pairs breed and rear larger broods

(Southern 1970, Delmée *et al.* 1978, Wendland 1984, Hirons 1985a, Petty 1992, Jedrzejewski *et al.* 1996). Among-year variation in the proportion of field voles in the diet of tawny owls in Kielder Forest was linked to vole abundance (Petty 1999). A similar response was exhibited to variation in the abundance of bank voles and yellow-necked mice *Apodemus flavicollis* by a population of tawny owls in a Polish primeval deciduous forest (Jedrzejewski *et al* 1994, 1996). Therefore, tawny owls show a functional, as opposed to numerical, response to variations in rodent density.

Tawny owls fulfil several of the criteria necessary for them to potentially play a role in the pattern of synchrony exhibited by field vole populations in Kielder Forest during 3-4 year cycles, which are spatially autocorrelated over distances of up to 6km (Lambin *et al.* 1998). They are an important and abundant predator of field voles (Petty 1999), range over a much larger area than their prey and have home ranges which encompass a number of clear-cuts (chapter 5) and exhibit a functional response to field vole abundance (Petty 1999). However, the shape of the functional response curve is important if owls are to regulate vole numbers. Resident generalists with alternative prey, such as the tawny owl, tend to stabilise rodent numbers (e.g. Andersson 1977). However, even though tawny owls in Kielder Forest caught an estimated 11-14% of the standing crop of field voles, there was no difference in variation in vole density between owl territories that were unoccupied, occupied with no breeding attempt, or occupied with a successful breeding attempt (Petty *et al.* 2000).

Petty (1992) stated that in Kielder Forest, "tawny owls obtained most of their food from clear-felled areas". This was inferred by the preponderance of field voles in the diet, and that the largest populations of field voles existed in grassy clear-cuts. In Kielder, field voles are absent from dense spruce plantations that lack grass cover (Thomson 1996). Southern and Lowe (1982) investigated tawny owl predation patterns by more direct means. Recovery of pellets containing the remains of rodents with metal leg rings showed that wood mice were preyed upon more heavily than bank voles, even though the latter were more abundant. This led to the suggestion that either the mice were the preferred prey, or they were more vulnerable to owl predation due to their preference for open habitats, or both.

This chapter aimed to provide direct evidence of the response of tawny owls to the spatial distribution and abundance of field voles, asking whether the variations in foraging behaviour of adult tawny owls were related to patterns of field vole abundance, and specifically:

1. Was foraging activity centred on habitat suitable for field voles?
2. Did field vole abundance affect foraging trip frequency and patch visit rates?
3. Was the length of time spent at patches related to their field vole densities?
4. Were larger movements rarer for birds with higher prey abundance in the areas that they used?
5. Was the proportion of field voles in the diet of individual owls related to vole abundance in foraging areas?

I acknowledge that a small sample and the difficulties outlined below (section 6.2.4) prevented me from achieving some of these aims.

6.2 Methods

6.2.1 Fieldwork protocol

Three adult male tawny owls with broods were radio-tracked in May and June of 1998. Each bird was followed continuously for 2-7.5 hour periods, and totals of 24, 25 and 31 hours. I attempted to keep up with owls, and so the movement rate of birds largely determined the variation in fix frequency, which was one every 3-33 (mean 14.8) minutes. The majority of locations were triangulated, with a resolution, in terms of forest structure, to the nearest sub-compartment (chapter 2), although birds were sometimes seen or located to the nearest tree.

When following active owls, signal strength often varied even though bearings remained the same. This was due to changes of antenna orientation as the bird moved, such as turning on its perch or pouncing. These activities were sometime difficult to differentiate from small changes of position. When consecutive error polygons overlap, it must be concluded that no measurable movement could be detected. (Springer 1979). Thus, changes of position were only noted when error polygons were separate.

6.2.2 Fix outlines, activity centres and field vole abundance

Polygon methods were the most suited to fitting activity centres to forestry stands and clear-cuts (see also chapter 5). Firstly, fixes within the immediate vicinity of the active nest box in each territory were excluded because they yielded no information on foraging behaviour. An arbitrary radius of 100m around each box was used rather than the entire plantation in which the box was located because nesting plantations bordered grassy habitat suitable for field voles and could, therefore, be used by foraging owls. A 100% minimum convex polygon (MCP) outline was drawn around the remaining fixes for each bird to delineate the entire area visited. Cluster polygons were then constructed using the appropriate percentage fix inclusion for each individual. This was determined using the excursion exclusion technique (Hodder *et al.* 1998), where the outer discontinuity in a plot of range area versus percent inclusion of fixes enables visual selection of the excursion-excluded core (EEC). Thus, 95% of fixes for bird 441, and 90% for birds 422 and 500 were included. Fixes excluded in the EEC cores were those furthest from the recalculated arithmetic mean fix, a measure based upon fix density (e.g. Robertson *et al.* 1998). Data were temporally autocorrelated and therefore, statistical considerations dictated the use of a non-parametric means of excluding fixes, such as by distance from nest boxes. However, this would have said little about the distribution of fixes in relation to foraging sites if they happened to lie further from nest sites and biologically, a measure based upon fix density was more meaningful.

Vole sign indices (VSIs) were performed at all grassy sites suitable for field voles within the limits of the movements of each owl to ensure coverage of the entire area that was used. The vole density in each MCP outline was estimated as the mean of VSI scores at the assessment sites that it encompassed. Polygon cores and outlines shared the same clear-cut patches and so it was impractical to look for differences in prey abundance between them. Instead, I compared the proportions of grassy habitat suitable for field voles inside cores, and the area remaining when cores were subtracted from MCPs, to investigate whether foraging activity was centred on such areas. These data were extracted from GIS coverages in a similar fashion to habitat data in chapter 5 (section 5.2.3).

6.2.3 Movement frequencies

Distances moved by birds at sampling intervals of ten minutes were placed into 22 one-hundred-metre classes ranging from 0 to 2.2 kilometres, and the frequency of movements in each class was calculated for each bird. Frequencies and movement distances were then log transformed and a linear regression model was fitted to each. Three pair wise MANOVA (multivariate analysis of variance) models were used to compare these regression slopes and test the hypothesis that relatively higher field vole densities in the areas by different birds used gave steeper slopes, as larger movements became progressively rarer.

6.2.4 Patch use and provisioning rates

Data were collected on the number of trips to and from the nest area made per night, the number of clear-cuts (patches) visited, the time spent at each patch and the mean vole density there. The nest area represented a central place, and for the purposes of trip rate calculations it was defined as the forestry stand in which the active nest box of each territory was located. In late June, males returned to this stand in order to provision fledged young, which were not necessarily located in the immediate vicinity of the nest box. Each "trip" started when the bird left the nest area, and terminated when it returned. Birds 441 and 500 had three-chick broods and bird 422 had a two-chick brood.

Owls regularly moved short distances between perches. To distinguish patch visits from chance locations in the process of travelling, a bird was deemed to have visited a patch if two or more consecutive fixes were located in or alongside it. A bird was said to be alongside a patch if a fix error polygon overlapped it, but was centred in a plantation rather than in the patch itself. The time of arrival was taken as the time of the first fix in a set of consecutive fixes, and the time of departure was taken as a movement from a patch to another area. The mean vole density was estimated as the average of those at VSI sites in a patch if there were more than one. This applied only to one bird. During some tracking periods, birds remained stationary or within the nest area for the whole duration of the period. Only data from tracking periods where owls left the nesting area at least once were included in analyses.

A closed-circuit time-lapse video camera system (Forestry Commission Research Division, Alice Holt Lodge, Surrey, UK) was employed at three nest boxes. These units were run for 0.5-14.5 (mean 9.94) hours. The contents of each videotape were viewed on a portable monochrome monitor, using the time-lapse facility of the video recorder to advance frames individually to aid the identification process. The number of deliveries per hour and the identity of prey, to the lowest possible taxonomic level, were recorded. Mean provisioning rates per box were calculated by dividing the total number of hours of footage at each nest box by the total number of deliveries per box.

Problems were experienced with illumination of nest boxes, in that the LED light unit supplied with the camera systems sometimes provided insufficient light to discriminate prey deliveries from other adult visits, or movements of large nestlings. Despite experimentation with other light sources, a large proportion of the tape footage was of insufficient quality for prey to be identified. Usable footage from a nest box video camera and radio tracking data for the male of that territory coincided only once during the study and therefore, direct comparisons between foraging behaviour and provisioning rates could not be made.

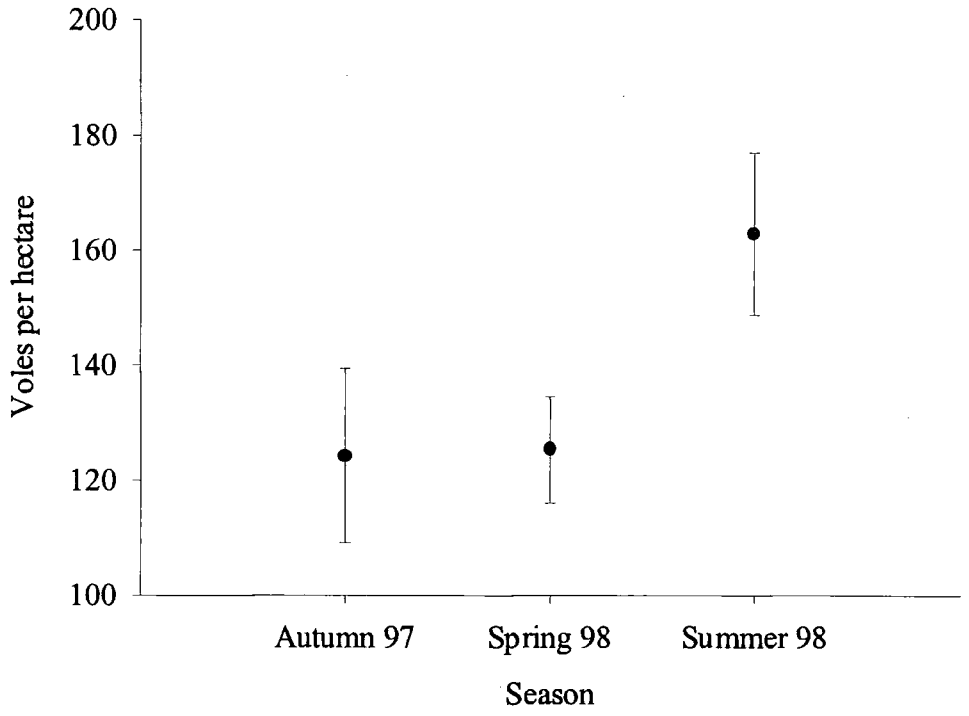
An automated colour photography system was field tested in tandem with the video units so that males, whose wings were dyed yellow with picric acid, could be distinguished from their mates. However, only rarely did the photographs show an owl with prey. Rain caused condensation inside the camera housing, which obscured some photographs. Powered by a car battery, the camera shutter was triggered by a modified domestic infrared transmitter and sensor system. This was sensitive to wind disturbance and false triggers were common. In addition, many photographs showed owls perched at the nest box entrance having already made a delivery.

6.3 Results

6.3.1 Data collected

Two hundred-and-sixty-three fixes were collected on three birds (bird 422 n = 100, bird 441 n = 73,bird 500 n = 90). Forty-two VSI assessments were conducted in suitable habitat throughout the areas visited by these birds. Usable video camera footage amounted to 79.5 hours, and 16 photographs from the automated still photography system showed identifiable prey items.

Figure 6.1. *Prevailing vole densities in Kielder Forest in autumn 1997 and spring / summer 1998 (S.J. Petty, unpublished data). Data shown were means of 20 assessment sites distributed throughout the tawny owl study area, with standard error bars.*



6.3.2 Prevailing vole densities

In summer 1998, vole densities in the tawny owl study area were high at an average of 162 (SE 14) animals per hectare (S.J. Petty, unpublished data)(figure 6.1).

6.3.3 MCP outlines and cores

6.3.3.1 Description of foraging areas

Bird 422 had widely separated foraging areas. The 100% MCP outline measured 121.58 ha and encompassed grassy habitat along unplanted streamsides, extensive mature forestry plantations, which included the nest area, and part of Kielder Village (figure 6.2). Exclusion of 10% of fixes created six polygon cores. The two largest cores included i) pre-thicket and mature forestry plantations, and ii) unplanted streamsides and mature forestry plantations. Of the smaller outliers, one encompassed exclusively unplanted streamsides, one exclusively pre-thicket stage forestry, one exclusively mature forestry, and the other a small area of broadleaved woodland and lawns in Kielder Village.

The 100% MCP outline for bird 441 measured 206.09 ha and stretched from a large clear-cut behind the mature forestry plantation in which the nest box was located, to an area of unplanted streamsides and clear-felled slopes of a sub-valley of the Kielder Burn (figure 6.3). This included plantation forestry and grazed sheepwalk on the higher ground between these areas. Exclusion of 5% of fixes to form cores split the MCP outline into two main activity centres, one at either end, suggesting that the large area between them was not heavily used, with the bird probably following the forest edge as it crossed the watershed. One core consisted entirely of clear-cut and the other mainly clear-cut with mature forestry and some agricultural land.

The 100% MCP outline of bird 500 measured 131.47 ha, enclosing three clear-cut patches and grassy roadside wayleaves, which supported some field voles. When excursive movements were excluded, the cores no longer included agricultural land (figure 6.4). The main core included three clear-cut patches, separated by mature trees and a road. Two outlying activity centres each included plantation forestry and part of a clear-cut patch. The area used was linear in nature, with the bird using roadside plantations to move from patch to patch. Thus, the ranging behaviour of

Figure 6.2. *MCP outline and 90% EEC cores (both green) for adult male 422. Open habitats are outlined in red, other land uses in black and streams in blue.*

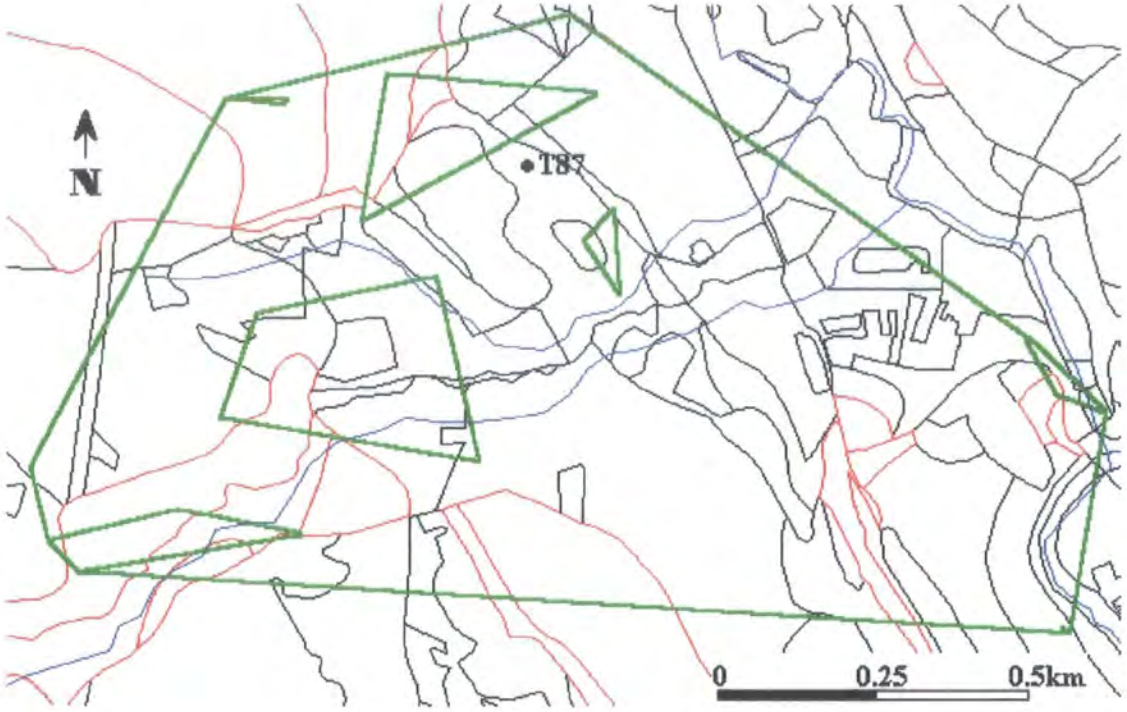


Figure 6.3. *MCP outline and 95% EEC cores (both green) for adult male 441. Open habitats are outlined in red, other land uses in black and streams in blue.*

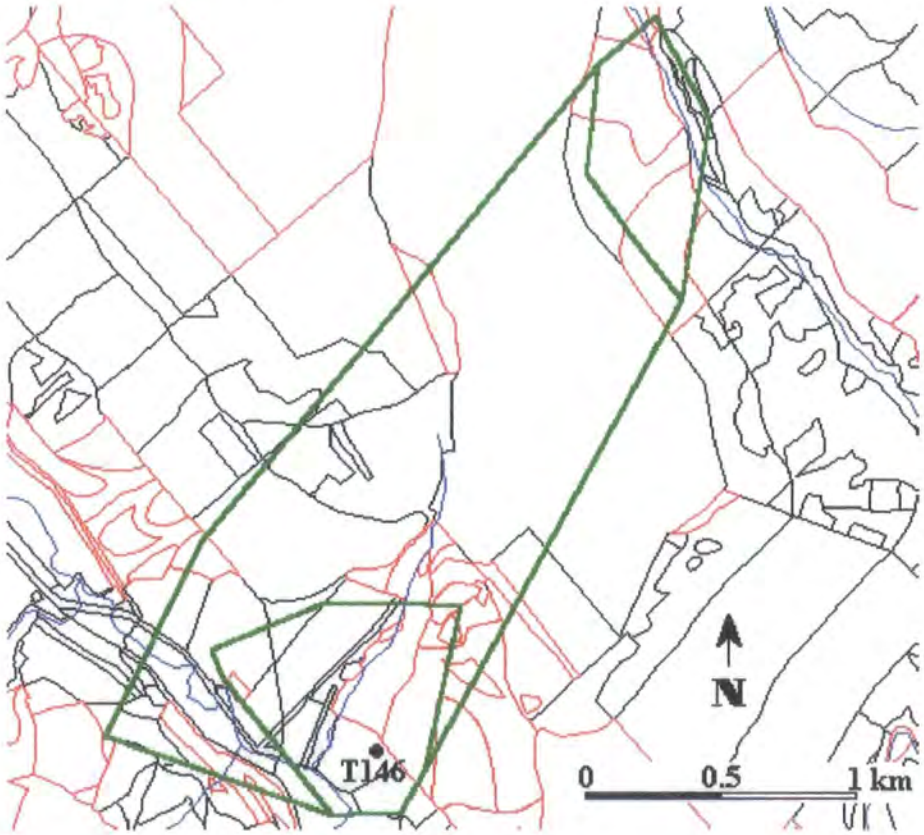


Figure 6.4. *MCP outline and 90% EEC cores (both green) for adult male 500. Agricultural land is outlined in blue, other open habitats in red, and other land uses in black.*

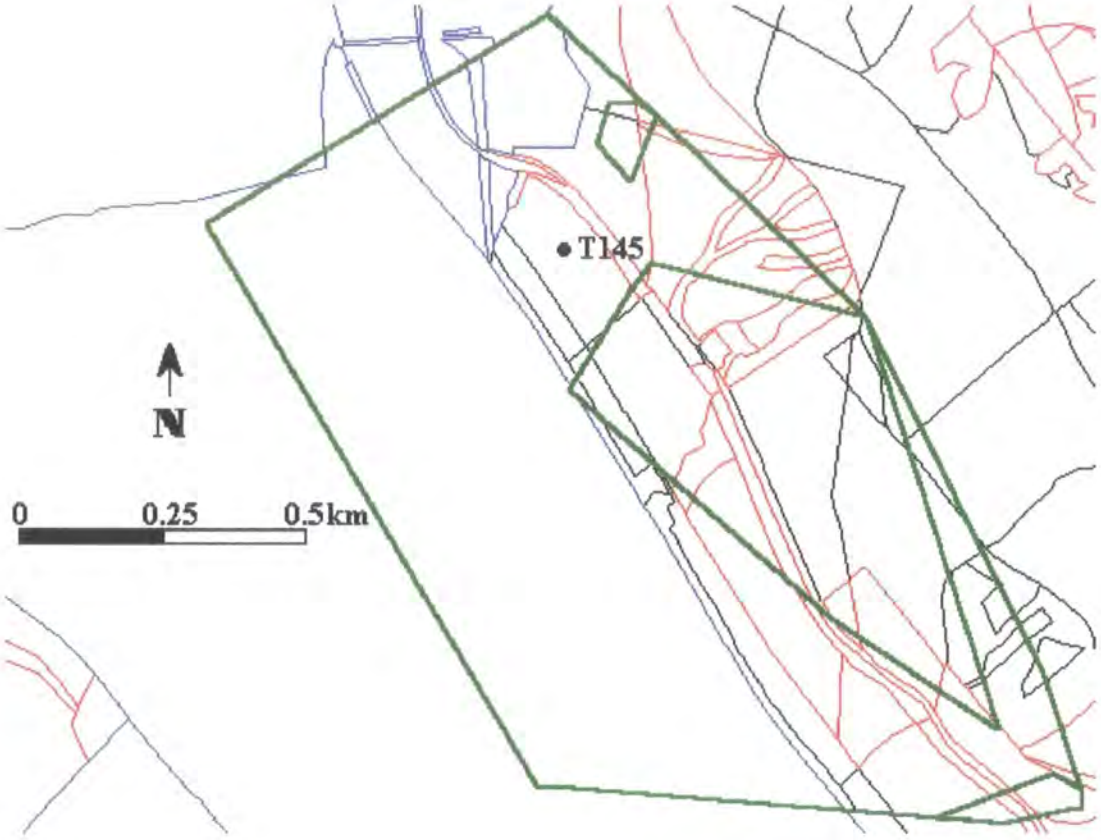


Table 6.1. *Areas and proportions of vole habitat of 100% MCP outlines with polygon cores subtracted, and of polygon cores for three adult male tawny owls radio-tracked continuously in 1998. Mean vole density estimates for 100% MCP outlines, with CVs among VSI sampling sites, are also given.*

Frequency	MCP, core subtracted		Core		Voles per hectare, MCP outline	
	Area (ha)	% vole habitat	Area (ha)	% vole habitat	Number	CV (%)
422	106.14	16.8	15.44	27.1	233	4
441	149.78	13.0	56.31	55.7	273	8
500	100.54	11.6	30.93	37.4	134	32

each bird was associated with feeding, nesting and roosting areas, and those that were used mainly when travelling between such areas.

6.3.3.2 Field vole abundance and habitat suitable for field voles

The mean field vole density estimate was highest for the MCP outline of bird 441 and lowest for that of bird 500 (table 6.1). Estimates of vole densities within MCP outlines were least variable for bird 422, which had two VSI assessment sites. The outline for bird 441 had three VSI sites at which vole densities varied relatively little, and that of bird 500 encompassed 10 assessment sites where vole densities were the most variable of the three birds (table 6.1). The vole densities in the outlines of birds 441 and 422 were considerably higher than the seasonal mean for the study area (table 6.1, figure 3.1).

The mean percentage of habitat suitable for field voles in MCP outlines with the core areas subtracted was 13.8 (CV 20%), compared with 40.1 (CV 36%) in cores (table 6.1). These proportions corresponded to respective mean areas of 16.3 (CV 25%) and 15.7 (CV 89%) hectares (table 6.1). Thus, activity centres contained a greater proportion of habitat suitable for field voles than the rest of the area visited did.

6.3.4 Patch use

6.3.4.1 Staying times

Three owls visited patches for 6-171 (mean 46.67, SE 6.61) minutes. The minimum value reflects the minimum time taken to relocate a bird after first being found on or alongside a patch by my definition. Overall, there was no significant correlation between patch vole density estimates and the length of stay (Spearman's Rank correlation coefficient, $r_s = 0.02$, $n = 35$, $P = 0.91$). This was also the case for individual birds (Spearman's Rank correlation coefficients, 422: $r_s = 0.24$, $n = 12$, $P = 0.46$; 441: $r_s = -0.47$, $n = 7$, $P = 0.28$; 500: $r_s = 0.09$, $n = 16$, $P = 0.73$). In addition, when staying times were grouped and averaged for each level of estimated vole abundance, the length of time stayed at a patch was not significantly correlated with the vole abundance there (Spearman's Rank correlation coefficient $r_s = 0.27$, $n = 13$, $P = 0.34$)(figure 6.5).

Figure 6.5. *The mean duration of visits to clear-cut patches by three adult male tawny owls in relation to estimated field vole density at each patch, ± 1 SE bars.*

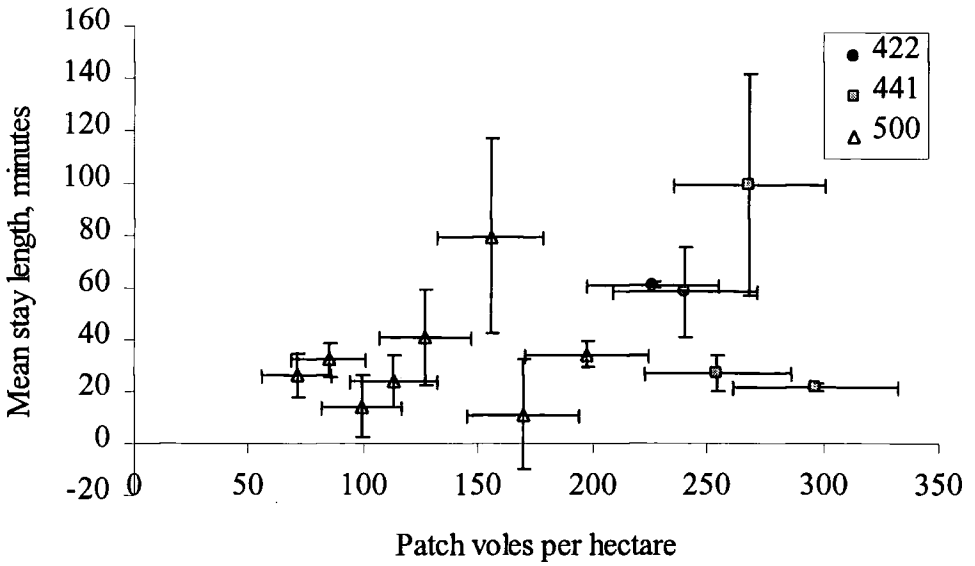


Table 6.2. *Trip, patch visit and delivery rates for three male tawny owls radio-tracked continuously in 1998.*

Nest box	Bird (frequency)	Mean trips per hour	Mean patches per hour	Mean deliveries per hour
T87	422	0.54	0.31	0.35
T146	441	0.61	0.74	0.60
T145	500	0.54	0.64	-

Table 6.3. *Three male tawny owls ranked by i) mean vole density within MCP outline, ii) brood size, iii) foraging trips per hour, and iv) patches visited per hour.*

Owl frequency	Brood	Vole density	Trip rate	Patch visit rate
422	2	2	2	3
441	1	1	1	1
500	1	3	2	2

6.3.4.2 Trip and patch visit rates

Overall, owls made between one and four (mean 2.67) trips per tracking session at rates of 0.19-1.00 (mean 0.60) trips per hour (table 6.2). During these trips, they visited 0.18-1.40 (mean 0.56) patches per hour. The owl with the highest mean field vole density estimate for its MCP outline (441) made the greatest number of trips per hour, visiting the greatest number of patches (tables 6.1, 6.2 and 6.3). However, for the other two birds, the respective ranks were interchangeable (table 6.3).

6.3.5 Movement frequencies

Small movements were far more common than larger ones (figures 6.6 and 6.7). All three log / log plots produced statistically significant linear regressions (figure 6.7)(422: $r^2 = 0.68$, $F_{1,7} = 12.57$, $P = 0.01$; 441 $r^2 = 0.55$, $F_{1,8} = 8.70$, $P = 0.02$; 500, $r^2 = 0.74$, $F_{1,8} = 19.91$, $P < 0.01$).

Paired comparisons showed that slopes and elevations were similar for birds 422 and 441 (MANOVA, slope: $F_{1,13} = 0.03$, $P = 0.87$; elevation: $F_{1,14} = 1.08$, $P = 0.32$), and for birds 441 and 500 (MANOVA, slope: $F_{1,14} = 1.15$, $P = 0.30$; elevation: $F_{1,15} = 0.43$, $P = 0.52$). However, the slope for bird 500 was significantly steeper than that of bird 422 (MANOVA, $F_{1,13} = 10.93$, $P = 0.001$). This difference was not associated with lower mean field vole density within the 100% MCP outline of bird 422 (table 6.1). In fact, field vole abundance was higher in the 100% MCP outline of bird 422 than that of bird 500.

6.3.6 Provisioning rates and prey taken

There were 79.5 hours of usable video footage taken over eight nights to give an average of 9.94 hours of footage per night. 40 hours were from nest box T87 (bird 442) and 39.5 hours were from nest box T146 (bird 441). The tapes from nest box T145 (bird 500) were all too dark to yield any useful data.

At nest box T87 (male 422), where the mean provisioning rate was 0.35 items per hour, the smallest number of deliveries was two in a 13-hour period, and the greatest was eight in a 14.5-hour period. At nest box T146 (male 441), the mean provisioning rate was 0.6 items per hour with a minimum number of deliveries of one in 30 minutes and a maximum number of 11 in eight hours. The higher mean provisioning

***Figure 6.6**. Frequency plot of movement distances at ten-minute sampling intervals for three adult male tawny owls radio-tracked continuously in 1998.*

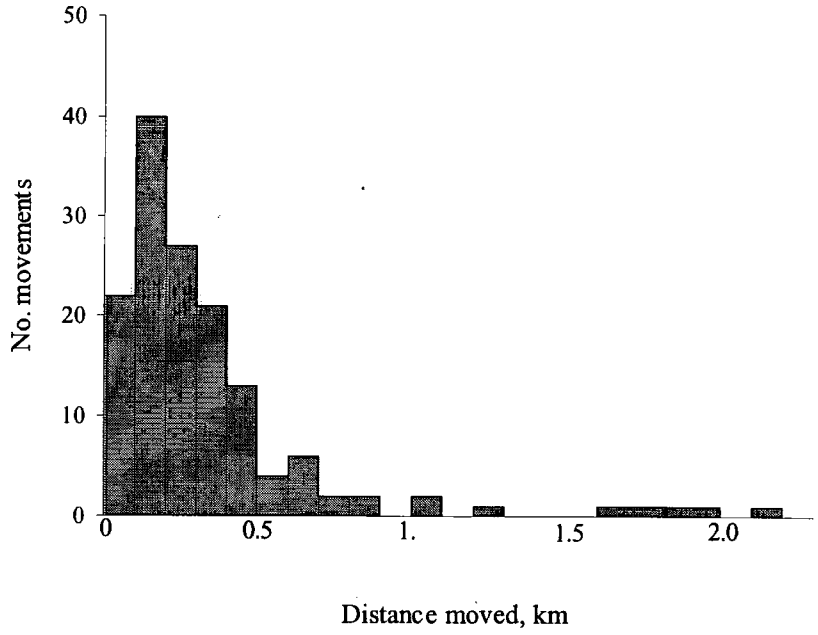
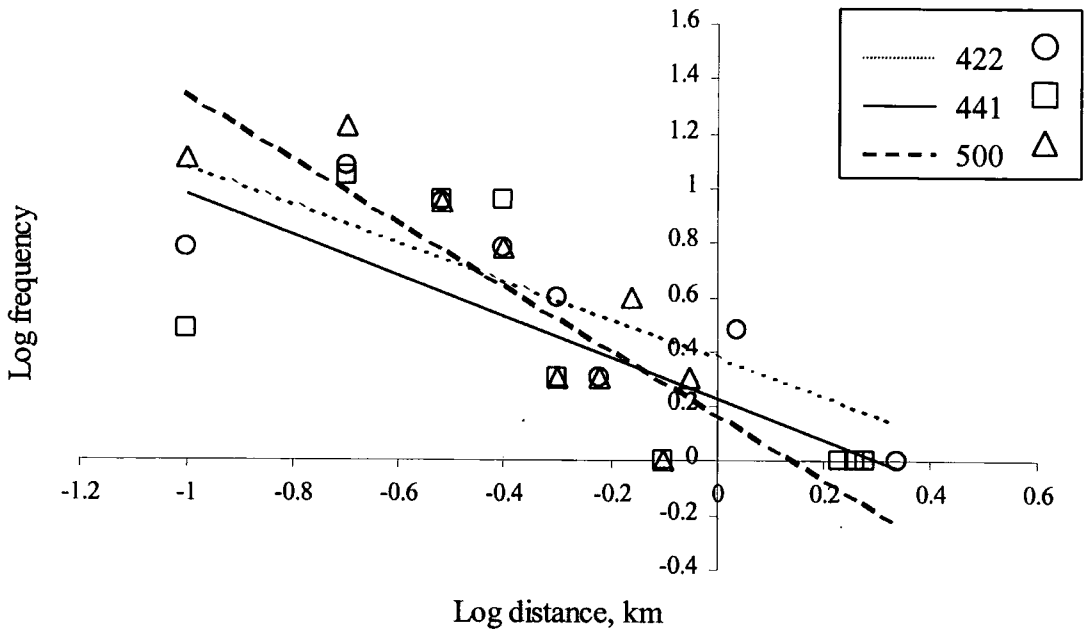


***Figure 6.7**. Log / log plot of the data shown in figure 6.6 with a linear regression line for each individual.*



rate at T146 corresponded with higher mean vole density in the MCP outline of the radio tagged male there. Due to the paucity of colour nest camera data, it was not possible using the monochrome video footage to distinguish which member of a pair made each delivery.

Of prey delivered to both nest boxes that could be identified to at least class level, most were field voles, roughly one quarter were shrews *Sorex* spp., and various other taxa formed smaller proportions (table 6.4). Although the proportion of field voles in identified deliveries was slightly higher at T146 (62.50%) than at T87 (57.14%), the mean vole density in the 100% MCP outline was higher in the male of box T87 (table 6.1), although the sample size was insufficient for statistical analysis.

Field voles constituted by far the largest proportion of biomass of prey identifiable to species level (table 6.4). The common frog *Rana temporaria* is heavier than the more numerous common shrew *Sorex araneus* and was more important in biomass terms. Field voles comprised 81.01% and 70.15% of the prey biomass delivered to nest boxes T87 and T146 respectively. Sixteen photographs taken by the automated still cameras showed an owl with prey (plate 6.1). Of these, 13 (81.25%) were voles (resolution was insufficient to discern which species), and there was one each of common frog, shrew species and wood mouse.

Table 6.4. *Prey items delivered to two tawny owl nest boxes, identified from video camera footage. Percentages were calculated as proportions of identified species only. Masses are in grams and biomass was calculated the nearest gram.*

		Frequency		Biomass	
Taxon	Unit mass	No.	%	Mass	%
Field vole *Microtus agrestis*[1]	28.1	16	59.3	450	79
Common shrew *Sorex araneus*[1]	10.2	3	11.1	31	5
Shrew species	-	3	11.1	-	-
Bank vole *Cleithrionomys glareolus*[1]	23.3	1	3.7	23	4
Rodent species	-	1	3.7	-	-
Chaffinch *Fringilla coelebs*[2]	22.0	1	3.7	22	3
Passerine species	-	1	3.7	-	-
Common frog *Rana temporaria*[1]	39.8	1	3.7	40	7
Unidentified	-	9	-	-	-
Total	-	36	100	566	100

[1]Mean weights of whole prey items from nests in Kielder Forest from Petty (1999).
[2]From Ratcliffe (1993).

Plate 6.1. *A photograph taken by the automated photography system. Using a hand lens, it was sometimes possible to identify prey, in this case a field vole (inset).*

6.4 Discussion

The conclusions that could be reached from this study were limited by the small sample size of birds radio tagged, and by small amounts of data yielded from nest observation techniques. In addition, owls were inactive for long periods, particularly in bad weather. However, I confirmed that much of the nocturnal activity of tawny owls when away from the nest area is concentrated around clear-cuts, or other grassy areas in the case of one bird, for which the nearest clear-cut was at some distance from the nest box (chapter 5, section 5.3.4.2, table 5.14).

Another problem with this study was temporal autocorrelation of data. The sample sizes of fixes derived from sub-sampling (chapter 5) were insufficient to show activity centres. The degree of autocorrelation would have been greater in foraging habitat than that used for travelling, due to slower movement rates when hunting. A high degree of temporal autocorrelation means that activity centres were indicative of areas in which birds spent more time, given that the sampling frequency did not differ according to where birds were located. I accept that the number of radiolocations was biased toward clear-cuts, and other grassy habitats suitable for field voles. However, Petty's (1992, 1999) large dietary data set, which shows the importance of field voles, and the fact that the most important field vole populations were in clear-cuts rather than forestry plantations (Petty 1992, Thomson 1996) together point to the importance of such habitats as foraging areas.

It was likely that the nocturnal deliveries of birds represented opportunistic predation of individuals at their roost sites within the forest. Petty (1999) lists a number of woodland bird species taken by tawny owls in Kielder Forest. Mature plantations in Kielder Forest also support small numbers of rodents (Ratcliffe and Petty 1986; also see Fernandez *et al.* 1994 for an account of rodent communities in the successional stages of Hamsterley Forest), such as the bank vole and wood mouse - species that were delivered to nest boxes in both this study and Petty's (1992). It was not possible to discriminate hunting from other behaviours that occurred within plantations and involved small changes in position. However, the small proportions of woodland prey delivered to nests indicated that little food was obtained from within the forest.

That there was no relationship between the vole density estimates in clear-cut patches and the length of time spent there was not an unexpected result given the limited choice of foraging sites and lack of variability in prey densities between them in two of the three territories studied. In addition, use of a patch was inferred if an owl was located alongside it, as well as locations that were on a clear-cut itself. This assumption was made because tawny owls hunt mainly from perches (e.g. Mikkola 1983), which were rare on clear-cuts. Observations using night vision equipment were attempted but proved difficult in this habitat, yielding little data from a large time investment. Further work using radio tags with activity switches may allow more precise interpretations of nocturnal activity, so that changes in bodily orientation associated with hunting from a perch could be discriminated from small movements or changes in position. Thus, it would be easier to discern whether an owl located along the edge of a patch was actually hunting there. Furthermore, use of a single VSI value for patches was potentially prone to error (Lambin *et al.* 2000, chapter 7) and ideally, large numbers of assessments or live trapping would have been performed in each patch. Unfortunately, time constraints did not permit this.

Alternatively, if owls found prey easy to come by, even at lower densities, their foraging activity may not have been influenced by spatial variation in absolute food abundance - a "natural satiation" hypothesis, as suggested by Lubin and Henschel (1996). In 1998, and in this area of Kielder Forest in particular, vole numbers were generally high and owls may not have discriminated between abundance and super-abundance of food.

Although no firm conclusions could be drawn on the effects of vole densities upon foraging effort, there was a suggestion that higher vole densities may be associated with a greater trip rate with an associated increase in both use of patches and nest box provisioning. However, the vole abundance data used were for the area within the outline formed by joining outer locations of radio tagged males, whereas prey deliveries would have also been made by females, for which no foraging data was collected. I found no evidence to suggest that the bird with two chicks put less effort into foraging than the other two birds, which had three-chick broods. There was no relative dietary response to vole densities by the two males for which video footage

was available, but for both this and the brood size comparison, much larger sample groups would be required for statistical analyses to be performed.

Viswanathan *et al.* (1999) gave examples of insect mammal and bird species that may optimise search efficiency by increasing the rarity of larger movements in response to higher food abundance. I found no evidence that the owl with the highest field vole densities in the areas that it used made relatively fewer large movements. Conversely, the bird that made the least number of large movements relative to small ones had the lowest vole densities in its foraging areas. Its territory was located in linear roadside habitats and it moved along plantations in small increments. In contrast, the other birds sometimes made larger movements across open ground because the habitat was patchier in the area that they used. Thus, to some extent, the size of movements between fixes may have been related to landscape structure.

Hansson and Hentonen (1988) hypothesised that demographic synchrony between both sympatric small rodent populations at the same locality, and between populations in different localities in the same geographical region, resulted from predation. Ydenberg (1987) and Korpimaki and Norrdahl (1989) suggested that synchrony in fluctuations among populations at a regional scale is caused by nomadic avian predators that specialise on small mammals. This theory has been termed the Regional Synchrony Hypothesis (Ims and Steen 1990). Inferred evidence from vole population dynamics in the presence or absence of tawny owls suggested that small-scale synchrony in field vole abundance was unlikely to be caused by avian predators (Petty *et al.* 2000).

The original design of this study involved simultaneous radio tracking, video camera observation and vole density assessment, so that prey deliveries could be attributed to tagged birds. This would also have enabled direct comparison of patch use, provisioning rates, prey composition and vole densities. With refinements to the designs of the video camera lighting unit (or use of a proven "off the shelf" automated photography system, which was beyond the budgetary constraints of this project), and a substantially increased sample size, such a study could yield high quality data to test hypotheses relating to functional responses and central place foraging theory, for example. Allied with intensive vole trapping, it would be

possible to quantify how much of the standing crop of field voles was removed by owls and how this affected vole populations, thus providing direct data to parameterise models built to determine exactly what effects predation by the tawny owl, a sedentary generalist predator, has on cyclic field vole populations.

6.5 Summary

This chapter examined the foraging behaviour of three adult male tawny owls in relation to the distribution and abundance of field voles. Small sample sizes and technical problems reduced its ability to reach firm conclusions, but the importance of clear-cuts and other grassy habitats suitable for field voles as feeding resources was confirmed.

Generally, nocturnal activity away from nest boxes was centred on clear-cuts (where most field vole populations were found), other grassy areas, and mature forestry plantations. The latter were used for travelling, roosting and breeding. Field voles constituted 59.3% of 27 identifiable deliveries to two nest boxes, corresponding to 79.5% of biomass. A small proportion of prey deliveries were of woodland species, suggesting that a limited amount of foraging may have also taken place within plantations.

The time that owls spent in patches was not significantly correlated with vole density estimates there. The use of activity switches on radio tags may have discriminated hunting on a patch from simply being located beside one and thus allowed patch use to be quantified more accurately. The hypothesis that the relative number of large foraging movements decreased with increasing food abundance at foraging sites was not supported. I suggest that, in this case, the relatively high number of small movements made by one individual with relatively low prey densities in the areas that it used was related to landscape structure.

A limited amount of evidence suggested that the numbers of foraging trips made, patches visited, and prey delivered to nest boxes was influenced by field vole abundance. I suggest a design for a study to quantify exactly what effects a sedentary predator has on the population dynamics of its main prey species.

Chapter 7 General discussion

7.1 Introduction

This chapter brings together the findings of chapters three to six, outlining some common questions and problems, putting them into a wider context, and reaching some general conclusions.

7.2 Synthesis

Redpath (1995) illustrated the effects of habitat fragmentation upon individuals in farmland. Kielder Forest was a much less fragmented environment. However, spatial heterogeneity has many different facets, including "reachability" of different parts of the habitat (de Roos and Sabelis 1995). Food abundance was another variable, with temporal variation, caused by cyclicity of field vole populations, creating contrasting levels of food abundance in the three years of the study.

The benefits of dispersal to tawny owls must be high, given its apparent costs, even without the additional burden of radio tags - most locally breeding adults were born in only one phase of the vole cycle, (Petty 1992). The belief that birds died if they were not recruited (Cramp 1985) was challenged by Petty's (1992) demonstration of a pool of unrecruited owls. I had hoped that radio tagged juveniles that were not recruited would become non-territorial "floaters" (e.g. Rohner 1996) and thus allow a comparison of their movements and behaviour with those of sedentary individuals. As juveniles reached independence and began to disperse, many succumbed to starvation, others were killed and yet more were lost. None were known to have been recruited. Therefore, it is likely that any floaters from these cohorts could only have come from the untagged groups which were not recruited, although there is a possibility that birds with which contact was lost had radios that failed prematurely and subsequently joined the non-territorial sector of the population. However, there were no radio tag failures for the groups of adults, which were studied using the same transmitters.

Consequently, I asked whether dispersing juveniles behaved rather like floaters in the way they moved through the forest, homing in on the areas of highest prey abundance. Food stress, evident from the high level of starvation, would have created

pressure to move on if prey were hard to come by, and indeed this was the case in the dispersal study.

Some of my results showed apparent dependency upon the temporal or spatial scale of the investigation. Thus, I compared short-term within-year patterns with longer-term between-year trends. In terms of spatial scale, the whole area familiar to an individual was considered separately to activity centres, for example. Thus, although home ranges of different sizes encompassed habitats in similar proportions to those available in the "local" environment, the division of time spent in different habitats by three males was far from equal. Therefore, clear distinctions were made when referring to the whole area familiar to an owl, and that which is most frequently used. This example highlights the importance of the way ecological questions are asked in interpreting the answers.

The assertion that the forest scale may be the most appropriate for investigating choices made by this population (chapter 5) is supported by data on the extent of juvenile dispersal movements (chapter 4), and has implications for studies of other wide-ranging populations. However, some questions relating to individuals or small groups may be more satisfactorily answered at a smaller scale. Many studies take place on dimensions smaller than the characteristic distance moved by an individual of a species over its lifetime, and the answers may be profoundly affected by the scale of investigation (e.g. Wiens 1989, May 1994). Practicalities usually restrict studies to arbitrarily defined limits. The questions asked should be appropriate to those limits. Questions of spatial scale are far from being solely of academic interest, with important applications reserve design, migration studies, and assessment of conservation status (May 1994).

In addition, this study also illustrated the importance of the interpretation results according to the exact methodology used. For example, the "home ranges" in chapter 5 were in fact cores calculated without the most unusual excursions. The cores used in chapter 6 similarly excluded unusual locations, but differed in that they were based upon data with a high degree of temporal autocorrelation and therefore, produced results which were at least partly related to the time spent in particular habitats.

In lowland broadleaved woodland, the tawny owl is regarded as highly sedentary and territorial, ranging over a relatively small well-known area (Southern and Lowe 1968, Southern 1970). In this upland environment, food supply was more centralised and birds covered areas that reflected its dispersion, with a striking degree of apparent overlap. Brown (1964) first introduced the concept of economic "defendability" of resources, where defence incurs costs as well as providing benefits. Given that vole densities varied among clear-cuts in adult foraging areas, it may be necessary for owls to include more than one clear-cut in the home range to ensure an adequate food supply. Defence of several clear-cuts for exclusive use is clearly less viable than excluding conspecifics from a small area of broadleaved woodland, particularly where one clear-cut is adjoined by several territories. In addition, dispersing juveniles roosted in occupied territories and presumably foraged nearby. The large amount of apparent overlap between home ranges of territorial adults, plus anecdotal evidence of patch sharing, supported the suggestion that territory holders do not tend to exclude other birds (juveniles, for example) from feeding areas. If Petty's (1992) unrecruited floaters are included, a postulated picture of much resource sharing emerges. It was unclear whether owls were aware of the presence of others, and there seems considerable scope for work on the dynamics of nocturnal interactions.

Thus, single species may show great adaptability and behavioural plasticity in the colonisation of new habitats. In addition to lowland broadleaved and upland deciduous habitats, tawny owls are also common in urban landscapes (Mikkola 1983, Galeotti 1994) and farmland (Hardy 1977, Redpath 1995). Specific ecological and behavioural adaptations are associated with the colonisation of each habitat. Such flexibility is mirrored by another widespread generalist predator, the red fox (Corbet and Harris 1991) and has been key to the success of both species, as landscapes have been progressively altered by anthropogenic activity. Thus, the ability of species to cope with such changes has clear implications for their conservation and management.

Both the juvenile dispersal and adult foraging chapters identified a need for vole abundance estimates over a shorter timescale than the one month minimum period over which changes in VSI scores can be observed. Given that prey resources were shared by a hypothetically large number of owls, there is considerable potential for

work on temporal trends in the pattern of resource use. Examples of potential questions include whether a threshold exists at which vole densities at a patch, or in a general area, no longer make it profitable to hunt there, how does this threshold change in relation to the number of other owls present, and do owls interfere with one another? The situation in Kielder Forest provides an unusual opportunity for predator-prey studies where prey populations are isolated within relatively well-defined boundaries and are readily quantifiable.

7.3 General problems

Small sample sizes restricted the power of some statistical tests and the scope of some analyses throughout this study. This was partly due to time constraints - for example upon the number of birds which could be radio tagged and the amount of data which could be collected for each - and partly to the nature of the study itself. High juvenile mortality and loss of contact reduced sample sizes in dispersal analyses, but in survival rate analyses, the effects of missing birds were ameliorated somewhat by the use of a technique that incorporated such data.

The VSI estimate of vole density is imperfect and, as with any calibration data, an element of error is involved in converting the frequency of fresh clippings to vole densities. Thus, table 2.2 (chapter 2) details the errors associated with single values, and the degree of variation between mean scores from multiple sites is detailed explicitly throughout the thesis.

Another potential source of error was observer bias. Each observer followed the exact procedure given in chapter 2, but an element of subjectivity in what constituted a fresh clipping was inevitable. There was also likely to be some local variation and so larger clear-cut patches were assigned multiple assessment sites, and scores were averaged.

Petty (1999) discusses the merits of abundance indices, giving examples of other studies that have used them with varying degrees of success. Lambin *et al.* 2000 pointed out that most long-term studies of cyclic vole populations rely on indices of abundance, and indeed, measures of density derived from live-trapping data are indices in themselves. They also stated that, although errors of estimates from single

values could be relatively high, those for measurements at the landscape scale (based upon 14 or more sites) should be minimal. It took around 30 minutes to perform each site assessment, so that the use of fewer than 14 sites was sometimes unavoidable due to time constraints. Quantification of prey availability is notoriously problematic. Despite their imperfections, VSIs generally show a strong relationship with trapping data (Petty 1992, 1999; Lambin *et al.* 2000) and remain relatively quick and effective estimators of relative prey abundance, even though absolute values may be subject to error. However, I accept that sampling and calibration errors, particularly where single values were used, may have explained the failure to reject null hypotheses in some cases. These instances were detailed in the relevant chapters, along with discussions of their limitations in relating prey abundance to availability.

7.4 Overview

The spatial approach taken, allied with the benefits of radio telemetry and modern computing techniques, gave a new insight into the way individuals respond to their environment – for example, to variation in prey abundance over space and time, and to the distribution of suitable feeding areas.. Studies of mortality are important in identifying which age groups or populations are particularly vulnerable (Newton 1979), and this was no exception. In addition, this study was the first to compare the effects of radio tags on juvenile owls using an untagged control group. Most studies discuss behavioural patterns in terms of long-term evolutionary processes. This work illustrated that, at least to some extent, individual decisions may be based upon shorter-term considerations, such as environmental conditions. Long-term empirical studies are rare (e.g. May 1994) and this work meant that tawny owls and field voles had been studied in Kielder Forest for a total of 20 years. Although tawny owls are generalist predators, this investigation highlighted the key importance of field voles, and the habitat supporting them, to many aspects of their ecology. It also highlighted the need to collect field data, and interpret the results of ecological studies in a manner appropriate to the question asked and the methodology used.

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